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EDITORIAL

As foreshadowed in our Editorial of September 1939, the exigencies of war have compelled some modification in the issue of this Journal. In particular, dates of publication have been rather irregular and the number of pages per number somewhat reduced. However, encouraged by the continued support received in the form of subscriptions forwarded and papers submitted, the Publication Committee have decided to continue their efforts to keep the Journal in being, in spite of considerable difficulties.

The present number is to be considered as a double one, covering the first two quarters of the year 1941, and it is confidently hoped to publish a second such double number at the close of the year or early in 1942, thus completing Volume XIX, for which the subscription will remain at 25s.

The contribution of suitable papers is still invited ; but, owing to the ever-increasing costs of production and the absolute necessity for strict economy in the use of paper, authors are most strongly urged to be as brief as possible without sacrificing essential matter or clarity and to reduce tables and illustrations to the very minimum.

B.T.P.B.
R.G.H.

STUDIES IN THE VARIATION OF NURSERY FRUIT TREES ON VEGETATIVELY RAISED ROOTSTOCKS*

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PART I. THE VARIATION OF ONE-YEAR-OLD APPLE AND PEAR TREES IN COMMERCIAL AND EXPERIMENTAL NURSERIES

Introduction.

It is well known that fruit trees of a single variety vary in their performance in the field. Not only are they variable in size, but also in cropping, rooting and general habit. These differences may appear in one or two-year-old trees in the nursery, or they may not become apparent until the trees come into bearing.

Although the use of clonal rootstocks has led to much greater uniformity in performance, trees on them still vary to some extent in size and crop. The elimination of wastage in the nursery and the production of a high proportion of saleable trees is of the first importance to the fruit tree raiser. To the research worker the production of uniform trees for experimental purposes is essential. Variable trees mean a waste of effort and ground, since the more the material varies the larger the number of trees required to attain a given standard of precision. If the groundwork for the desired uniformity could be laid down in the nursery, much wasteful grading out of unsuitable trees might be avoided. It is evident, therefore, that if this variation could be further controlled the work involved would be well worth while.

The writer is well aware that the consideration of these problems has tempted many investigators (especially in the U.S.A.) to work on the subject, though in the vast majority of cases the rootstocks have been of seedling origin. The literature of the subject arising from these investigations has been carefully studied and a bibliography of some thirty papers prepared, but owing to exigencies of space this is omitted, only those papers of most immediate importance to the present experiments being definitely referred to. The full bibliography is available if needed.

Apart from the effects of environment some variation is always inherent in the trees. This may be due to several factors, among which are differences in

* These studies were carried out during a period of residence at East Malling Research Station, Kent, England, and the present paper is part of a Thesis approved for the Degree of Doctor of Philosophy in the University of London.

the age, size and rooting of the rootstocks, previous history of the bud or the graft-wood and differences in the manipulative methods used in budding and grafting. The extent of this variation in nursery trees is examined in the first part of this paper. In the second and third parts, experiments designed to show how far small differences in rootstock and scion may influence the tree in the early stages of its existence are described.

1. IN A COMMERCIAL NURSERY.

The first attempt in this investigation to measure the amount of variation in young trees consisted of a survey of a large commercial nursery, which included five varieties of apples, on five different rootstocks, and three of pear, all on Quince A.

The different kinds of apple trees ranged in average height from 52 cm. to 100 cm. and the pear trees from 68 cm. to 101 cm. The coefficients of variability* were calculated for each group of similar trees and varied from 17·5 to 45·0 in the apples and from 19·5 to 26·6 in the pears.

Rootstock and scion variety influenced both the average height and the variability of the trees. However, it was evident that other uncontrolled factors, such as soil and proximity to full grown trees, also had a marked influence, so that the data obtained could not supply reliable indications of particular rootstock or scion potentialities.

2. SEASONAL DIFFERENCES IN "TAKE", HEIGHT AND VARIATION IN AN EXPERIMENTAL NURSERY.

It has long been realized that the success of budding and the growth of nursery trees varies in different seasons. To gain some knowledge of the variation due to this seasonal factor and to obtain more reliable data as to the effect of rootstock and scion variety, a study was made of the records of "take" and height of maiden trees over a period of five years, i.e. four budding seasons. The records were obtained from an experimental nursery at East Malling Research Station in which the effects of environment were as far as possible controlled. The first planting was made in 1933, and the trees were budded in the summer of 1934. The succeeding years' trees were planted according to the same plan in adjacent plots.

Three varieties of apples, Cox's Orange Pippin, Bramley's Seedling and Worcester Pearmain were budded each year on Malling rootstocks Nos. I, VII, IX and XVI. There were four plots each of the varieties on No. IX and two of those on each of the other rootstocks, each replicated plot being made up of twenty-five trees. The study included three pear varieties, Conference, Durondeau

* The coefficient of variability (V) is the standard error of a single observation (standard deviation) expressed as a percentage of the mean.

and Pitmaston Duchess, budded each year on two quince rootstocks, Malling A and C.

In the following discussion the term " take " denotes the number of buds that resulted in trees, expressed as a percentage of the total number of rootstocks budded. The average maiden height is given to the nearest centimetre. Variation is expressed by the coefficient of variability.

An attempt was made to correlate records of temperature, sunshine and rainfall with the factors mentioned above, these records being made daily over the four seasons. However, the period under review was not long enough to enable any relationship to be established between any particular climatic factor and either take or growth.

Take of buds. The average take of apple buds varied from 61% and 65% in 1934 and 1935, to 97% in 1937. Of the three varieties, Bramley's Seedling gave the highest take except in 1935. While 1934 was poor for all varieties, it seems probable that some factor other than season was responsible for the remarkably low take of Cox's Orange Pippin (45%) in that year. Trees on No. XVI rootstock varied most from year to year, giving particularly poor results in 1934 and 1935, but the best of all in 1937. The smallest seasonal differences were found in trees on No. IX rootstock.

Varietal and seasonal differences were smaller with pears than with apples. The take was lowest in 1935 (82%), but was over 90% in the other three years. Conference averaged the best in the four seasons, while Pitmaston Duchess was the poorest. The range in take over the four seasons was less on Quince C than on Quince A.

Growth. Unlike take, the range in height over the four seasons was smaller with apples than with pears. Least growth was made by all trees of apple varieties budded in 1935 and 1936, except Cox's Orange Pippin which was low only in 1936. This variety always made more growth than the other two. Worcester Pearmain varied most from season to season. Trees on all rootstocks followed the same general trend except those on No. IX rootstock, on which least growth was made by trees budded in 1937. Trees on No. XVI were exceptionally small when budded in 1936 (85 cm.) in which season they made even less growth than trees on No. IX (91 cm.).

Of the pears, Pitmaston Duchess trees were the smallest throughout, and they had a much greater range in height over the four seasons than trees of Conference and Durondeau. The average growth of this variety in 1935 was only 59 cm. Trees on Quince C were always somewhat taller than those on Quince A, but the seasonal response was alike on both rootstocks.

Variation. On the whole, the pear trees varied more than the apples. The average coefficients of variability for the height of all varieties and rootstocks ranged from 20·4 to 27·5 for the former and from 11·4 to 17·0 for the latter.

Seasonal differences were similar for both kinds of fruit tree, the most variable trees being produced in 1935 and 1936.

The three apple varieties behaved alike from season to season and appeared to be about equally variable. The trees on No. IX showed the least effect of season, the coefficients of variability ranging from 11·8 to 14·2, while those on No. I fluctuated most, showing the greatest variation in 1935 (V=25·2) and the least in 1937 (V=9·5).

Much more marked varietal differences were shown by the pears. Conference trees varied very much less than the other two varieties, except in 1935, and Pitmaston Duchess was always the most variable, especially in 1935. Durondeau, on the other hand, showed little change from year to year.

The trees on Quince C were always less variable than those on Quince A and showed less seasonal fluctuation.

It should be noted that variation, as measured by the coefficient of variability, was generally negatively correlated with growth from season to season. Thus, the two more variable seasons 1935 and 1936 were also those in which least growth was made. This was true for both apples and pears. It may, therefore, be expected that under conditions favouring growth, variation will be small, and under those less favourable to growth, variation will tend to be higher.

3. Growth and Variation during the Growing Season.

The growth of both apples and pears on certain rootstocks was measured weekly, and the growth curves were compared to examine the effect of variety and rootstock on growth during 1938.

The material for this study was that in the experimental nursery, budded in July 1937. Growth curves obtained for the three varieties on Nos. IX and XVI are shown in Fig. 1. There appears to be little or no difference between the varieties generally. The one making the greatest amount of growth, viz. Cox's Orange Pippin, did not continue growth later in the season. The smaller size of the trees made by the other two varieties appears to be due to a slowing down rather than to an earlier cessation of growth.

The most striking difference is due to a rootstock effect. From the plotted curves, it is seen that those for trees on No. IX flattened out earlier than those for trees on other rootstocks, i.e. from the middle of July onwards. Growth itself actually ceased only about a week earlier and little change was to be seen in the relative heights of the trees on different rootstocks after September 30th, although growth continued for another two weeks. Differences between pears were not very clear, but Pitmaston Duchess was much slower growing than Conference and Durondeau all through the season.

Figure 2 shows the variation through the season of apple varieties on Nos. IX and XVI. Generally, both curves show the same form ; variation is

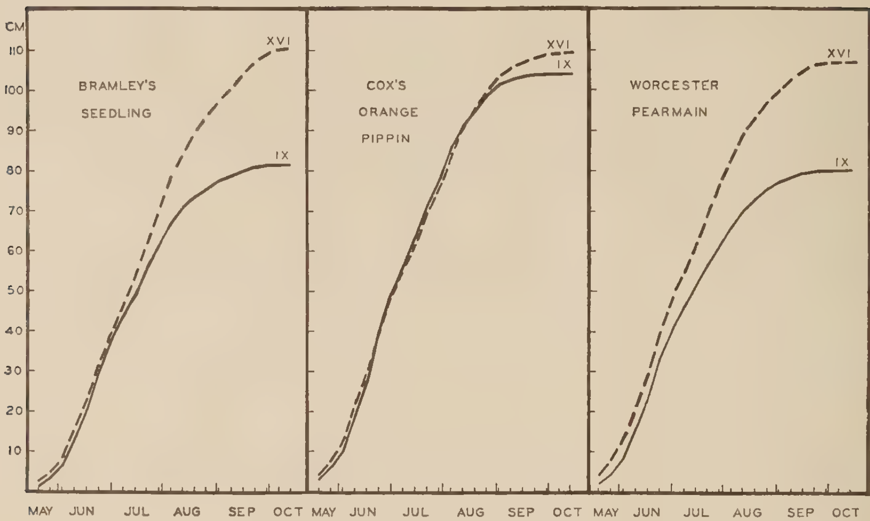


FIG. 1.

Growth curves for three varieties of apple on two clonal rootstocks: Malling Nos. IX and XII.

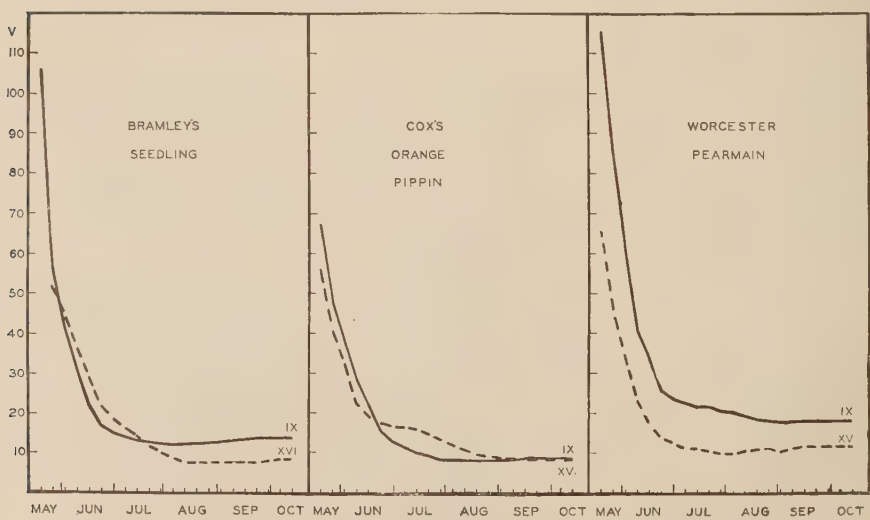


FIG. 2.

Curves showing the changes in variation in growth of three apple varieties on two clonal rootstocks in the course of the growing season.

very high at the beginning of the growing season but drops very rapidly to a point where the curve flattens out, beyond which little change takes place. The time or point at which variation becomes stabilized varies over a period extending from the first week in July until about the middle of August. There appears no essential difference between the three varieties and the four rootstocks, with the exception of Bramley's Seedling and Cox's Orange Pippin on No. XVI. The curves for these two do not flatten out until approximately a month later than those for other combinations. Trees on No. IX were more variable early in the season than trees on other rootstocks, but they did not necessarily remain so over the whole period.

In Fig. 3 the coefficients of variability for pears are plotted week by week. The main difference is between varieties. Though all show that variation greatly decreased during the season, Conference was much less variable early in the season than the other two varieties. This difference persisted throughout, but by the time growth ceased was comparatively small. Variation in Conference became practically constant after six weeks' growth, eight weeks earlier than in the other varieties.

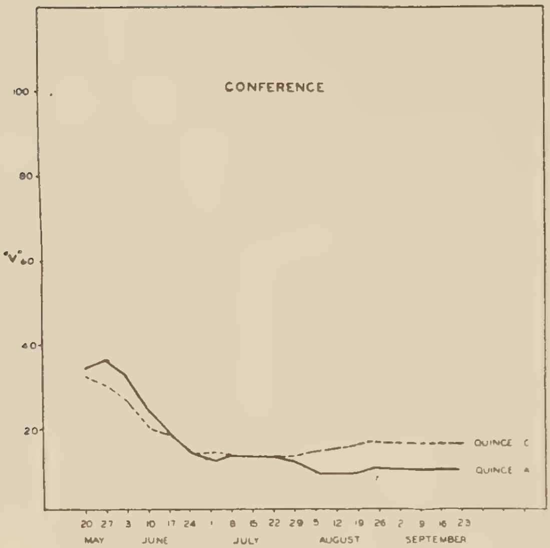
Weekly Increment in Growth.

The most striking result brought out by examination of the weekly growth increments is the occurrence of a double peak; this is illustrated in the histograms in Fig. 4, which show the weekly increments of Bramley's Seedling on Nos. IX and XVI. These are typical of the other combinations of variety and rootstock. The reason for the second peak is, it appears, the sharp rise both in temperature and hours of sunshine during those weeks. Other factors, such as soil moisture, showed no relation whatever to weekly fluctuations of growth. From this it may be assumed that there was sufficient moisture in the soil to enable normal growth processes to proceed. The histograms also show that the greatest fluctuations occurred before and during the period of peak growth.

With trees on No. IX, deviations from the normal were slightly less than with other apple and quince rootstocks. This was particularly evident after the first peak of growth had been passed.

4. RELATION OF TIME OF BUD-BREAK TO ULTIMATE SIZE OF TREE.

In the foregoing study it has been shown that variation is very high at the start of the season. This is probably connected with variations in the time at which the buds start to grow. The question arises, then, whether buds which begin growth early make larger one-year-old trees than those in which the start of growth is delayed. To decide this point careful observations were made of the time of bud-break, over an eight week period, of 36 trees each of Cox's Orange



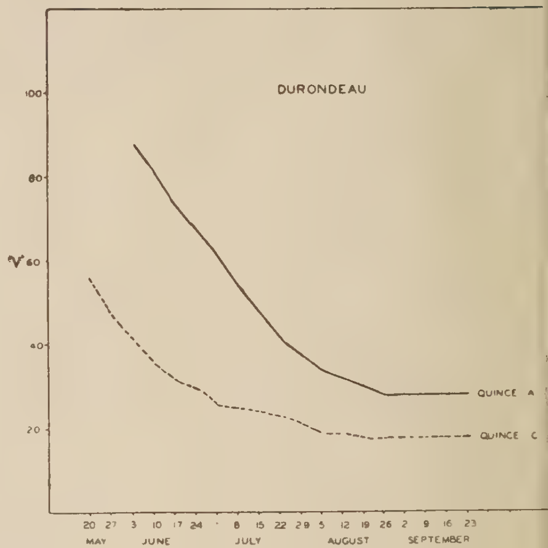
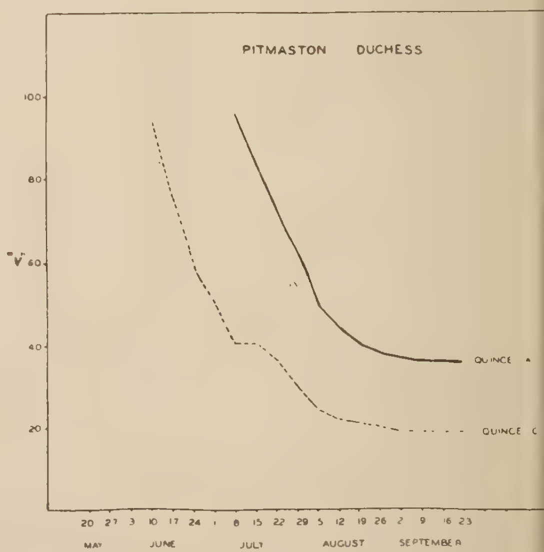


Fig. 3.
Curves showing the change in variation of pear trees during the growing season; three varieties on two quince rootstocks.



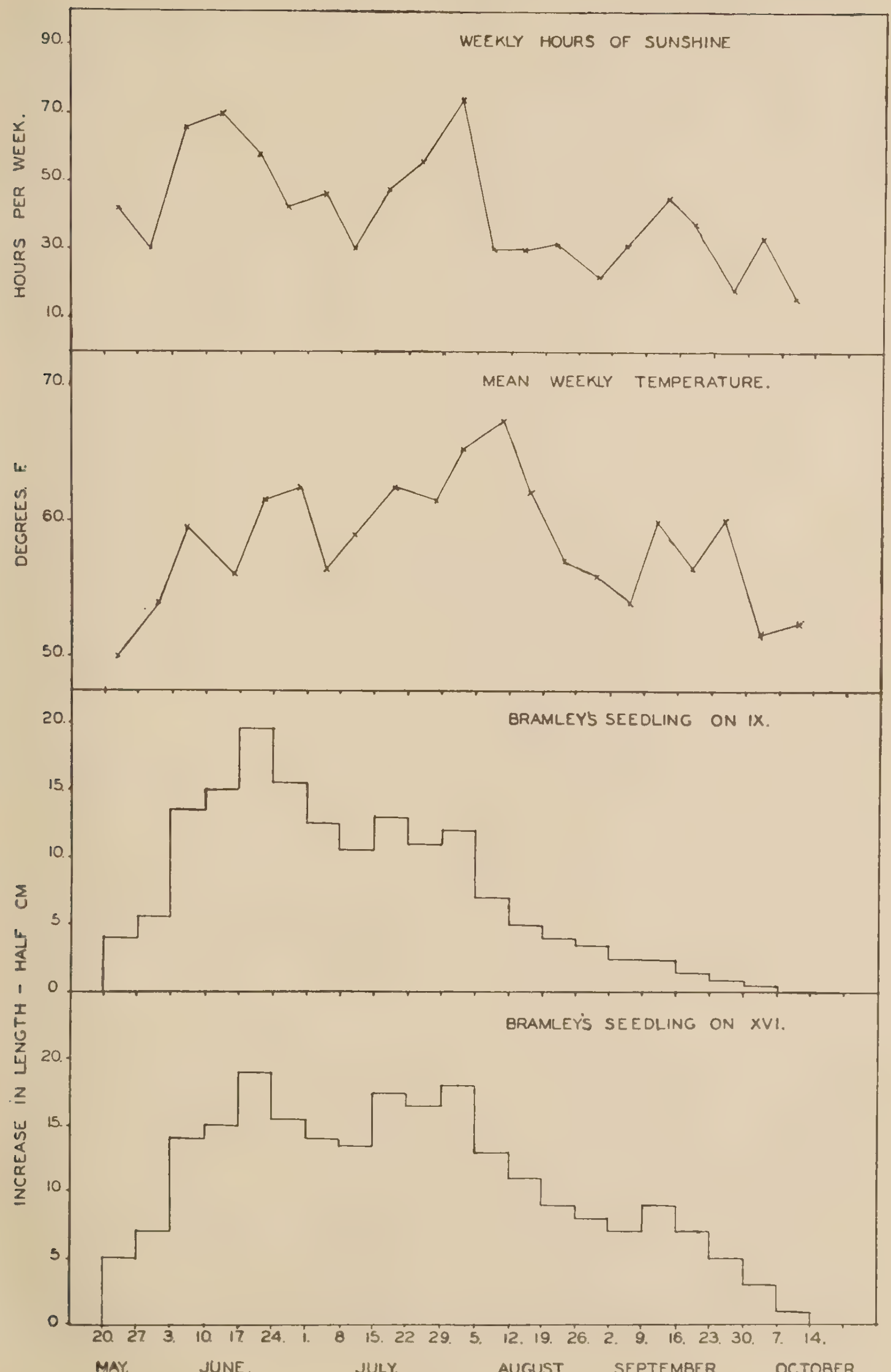


FIG. 4.

Diagram showing the relation between the weekly increment in growth of Bramley's Seedling, on two rootstocks, and sunshine and temperature.

Pippin and Grenadier, on six different rootstocks. Table I illustrates the connection between the week of bud-break and the maiden height of all uninjured trees. In this Table the t rees are grouped according to height and week of bud-break.

TABLE I.

Distribution of Trees showing Relation between Maiden Height and Time of Bud-break.

Maiden height (cm.).	Week of bud-break.							
	1	2	3	4	5	6	7	8
50-69	—	—	—	2	1	1	—	1
70-89	1	4	13	6	3	2	—	1
90-109	12	13	40	10	8	1	1	9
110-129	25	11	11	3	—	—	1	1
Over 130	4	5	6	1	—	—	—	—
Total number of trees	42	33	70	22	12	4	2	12

By the end of the third week most of the buds had begun growth and the largest trees were those whose buds began growth during this period. It is evident, also, that no small trees began bud growth until after the third week. The correlation coefficient expressing the relationship between week of bud-break and height, was found to be —0·3695, a value which, though not very high, is highly significant ($P < 0 \cdot 001$).

5. EFFECT OF INJURY TO GROWING TIP ON VARIATION.

It sometimes happens in nursery practice that growing shoots suffer injury to the tip, either by accidental breakage or by caterpillar attack.

The records of five combinations of apple variety and rootstock in the experimental nursery, budded in 1935, which suffered from caterpillar attack early in the season, were examined. They included Bramley's Seedling on Nos. I, VII and XVI, in which the proportions of trees injured were 30%, 33% and 69% respectively, Cox's Orange Pippin on IX (39%) and Worcester Pearmain on I (21%).

On the whole, the inclusion of the injured trees made little difference to the average height, with the exception of the extensively damaged Bramley's Seedling on No. XVI, where the mean height of the undamaged trees was significantly greater than for the whole. On the other hand, the inclusion of the injured trees of Cox's Orange Pippin on No. IX actually raised the average height above that of the undamaged trees.

On the whole, the exclusion of injured trees lowered the variation slightly throughout, but in no single instance was the difference statistically significant.

It must be remembered that these results apply only when the injury takes place early in the growing season, and only to growth in the first season.

PART II.—VARIATION IN ROOTSTOCK CLONES AND ITS EFFECT ON SIZE OF BUDDED TREE.

Although clonal rootstocks are produced asexually and are thus free from seedling variation, the actual shoots when removed from the stools or layer beds wherein they are multiplied vary considerably in size and rooting. It is also known from observation that the time of bud-break on the stool extends over several weeks. The question arises, then, whether any relationship exists between these two factors, and whether or not either of them bears any relation to the position of the shoot on the stool itself. Shoots which are not of suitable size for budding in the following summer or are not well rooted are generally bedded out for another year, so that they are one year older at budding time. Owing to the extra year's growth these bedded stocks may be less variable in size and rooting at budding time, and also larger and better rooted.

1. THE EFFECT OF TIME OF BUD-BREAK ON SIZE AND ROOTING OF INDIVIDUAL STOOL SHOOTS.

Ten five-year-old No. I, ten eleven-year-old No. XII apple and six eight-year-old Quince A stools in the Station's nursery were examined weekly, and the buds marked by numbered wire stakes as they appeared. It was impossible to mark all the quince buds owing to the large number of buds on each stool. Later the stake was replaced by a tag attached to the shoot itself. The stools were earthed up throughout the season in the normal way and in the autumn were unearthed and all shoots removed. An attempt was made at this time to note whether differences in position on the stool were connected with size, but no correlation was observed. All shoots (30 No. I, 128 No. XII and 124 Quince A) were then graded for amount of rooting, the Grade into which each shoot was placed being determined by the proportion of roots relative to the size of the shoot.

Results.

The three rootstocks differed in the period during which buds started growth as follows: Quince A, 3-4 weeks; No. I, 3-7 weeks, and No. XII, 6-7 weeks.

No indication of any correlation between time of bud-break and size (length and diameter) or amount of rooting was revealed. In this respect the rootstocks behaved differently from the budded trees previously described (Part I).

A significant positive correlation was found between length of shoot and amount of rooting in No. XII (+0·6171) and in Quince A (+0·4417). It was thus evident that larger shoots were better rooted than smaller ones. The correlation between length and diameter was very high, +0·9321 for No. XII

and +0·8560 for those of Quince A. These figures show that either measurement gave a good indication of shoot size.

2. Comparison of Variation in Size and Root Development of Layered and Bedded Rootstocks.

To investigate the comparative variability in size and root development of rootstocks taken straight from the stool and those bedded for a second season, 200 layered and 200 bedded rootstocks each of Malling No. I and Quince A were selected at random.

Each sample of 200 was then sub-divided into four Grades for amount of rooting, and the diameter of each stock was measured to the nearest millimetre below the calipers setting. All stool shoots were included, whether they were suitable for budding in the following season or not.

Results.

The results for stock diameter are summarized in Table II.

Table II.

Mean Diameter and Coefficient of Variability of One-year-layered and Bedded Rootstocks.

Kind of Stock.	Mean Diameter (mm.).		Coefficient of variability.	
	No. I.	Quince A.	No. I.	Quince A.
One-year-layered ..	4·1	4·5	32·1	24·8
Bedded	7·1	8·7	17·6	15·7

With both No. I and Quince A, bedded stocks were significantly larger than one-year-layered stocks and much less variable. ($P<0·001$ in all comparisons.)

Table III shows the distribution of stocks in four root Grades. Grade 1 includes stocks or shoots which had failed to root, while Grade 4 includes the heavily rooted stocks.

Table III.

Distribution of Stocks in Different Root Grades.

Root Grade.	No. I		Quince A.	
	One-year-layered.	Bedded.	One-year-layered.	Bedded.
1	31	0	16	0
2	96	0	108	2
3	47	74	54	45
4	26	126	22	153

Differences in rooting between layered and bedded stocks were considerable. While the layered stocks were distributed over the four root Grades, the majority of bedded stocks were in the heavy-rooted Grade with only two stocks in Grade 2 and none in the non-rooted Grade. There was little difference between No. I and Quince A, except more layered No. I in Grade 1 and more bedded Quince A in Grade 4.

Thus, in this particular year, the bedded rootstocks examined were larger and better rooted than the one-year-layers. As these are typical of the general run of such stocks it may be concluded that this result is generally true. It should be emphasized, however, that the one-year-layered stocks included the whole produce of the stools, only a part of which would be considered fit for immediate use.

3. Effect of Variation in a Clonal Rootstock on Size of Budded Tree.

The variations in size and rooting of clonal rootstocks having been examined and measured, it remains to investigate their effect upon tree growth. The following two factorial experiments were carried out on (i) Cox's Orange Pippin apple on No. I and (ii) Conference pear on Quince A. Each experiment was designed to compare the effect of three factors affecting the rootstock : (*a*) *Age*—layered as against bedded stocks, (*b*) *Size*—in which rootstocks of three diameters were compared, and (*c*) *Amount of rooting*—comparing well and poorly rooted stocks. Thus, twelve different kinds of rootstock were compared.

Experimental Design.

Each experiment consisted, in the first place, of eight randomized blocks, each containing two plots each of 30 rootstocks, the one being one-year-layered and the other bedded.

Each of these plots was sub-divided into six sub-plots, each of five rootstocks, among which the six combinations of size and rooting were distributed at random. This gave 96 sub-plots in each experiment. This design has frequently been used in horticultural experiments and was described by Yates (1937). The effects of size and amount of rooting, which might, perhaps, be expected to show comparatively small differences, are compared with greater accuracy than those due to the different ages of stocks.

Grading of Rootstocks.

Both layered and bedded rootstocks were graded as follows, only rootstocks suitable for budding being used : The rootstocks were first separated into three Grades according to the amount of root development. The middle Grade was then discarded to avoid overlapping and to give a comparison of the two extremes. Each rootstock was measured for diameter at a point approximately nine inches

above the base and mid-way between two nodes. Three size Grades were thus obtained for each Grade of rooting and for both one-year-layered and bedded rootstocks.

The first Grade of both bedded lots overlapped Grade 3 layers, and the diameter Grades of bedded No. I did not correspond with those of bedded Quince A. This was unavoidable owing to the difference in size and variation between one-year-layered and bedded rootstocks and the fact that the bedded Quince A were, on the whole, slightly larger than the bedded No. I rootstocks. All were planted out in January 1938 and budded in the following July.

Records.

Records of rootstock diameter were taken in the spring of 1939, before buds had started to grow, to determine whether rootstock differences had persisted. The heights of the maiden trees were measured at the end of August. At this time the trees were still growing ; but as any differences likely to occur would be apparent at that time (as previously reported, variation in trees was by then almost constant), it was felt that this procedure was fully justified.

Results.

1. Apples.

(*a*) *Rootstock Diameter at the Start of the Growing Season.*

The analysis of the measurements showed clearly that there was still a significant difference between the size of the one-year-layered and the bedded rootstocks, 8·5 mm. for the former and 9·8 mm. for the latter, the appropriate standard error being 0·38 mm. It was noted, however, that the relative difference was not as great as when the rootstocks were planted a year previously.

TABLE IV.

Mean Diameter of Rootstock (mm.) : No. I.

Amount of Rooting.	Original Diameter Grade.		
	1	2	3
Well rooted	9·0	9·2	10·4
Poorly rooted . .	8·1	8·8	9·4

Difference necessary for significance, 0·5 mm. (P=0·05).

There were now also definite differences due to both size and rooting (Table IV). Well rooted stocks of the same original diameter as the poorly rooted ones were now considerably larger.

(*b*) *Height.*

In spite of the differences noted above, the heights of the one-year-old trees showed no significant differences in any of the three comparisons. That is, different ages of rootstocks (i.e. one-year-layered and bedded), the amount of rooting and the size of rootstock had no apparent influence on tree size.

2. Pears on Quince.

(*a*) *Rootstock Diameter at the Start of the Growing Season.*

By the spring of 1939, one-year-layered rootstocks, which were originally smaller than corresponding bedded rootstocks, had evidently made more growth, so that, at this time, both were approximately of the same size.

TABLE V.

Mean Diameter of Rootstock (mm.): Quince A.

Amount of Rooting.	Original Diameter Grade.		
	1	2	3
Well rooted	11·3	11·7	12·4
Poorly rooted ..	10·6	11·3	11·7

Difference necessary for significance 0·4 mm. (P=0·05.)

There were significant differences due to both size and rooting (Table V.). As with apples, well rooted stocks had now become larger, though originally they were the same size as poorly rooted ones.

Although, on the average, there was no difference in size between one-year-layered and bedded rootstocks, there was a difference within two of the three size Grades. (Table VI.)

TABLE VI.

Mean Diameter of Stock (mm.): Quince A.

Age of Stock.	Original Diameter Grade.		
	1	2	3
One-year-layered ..	11·0	11·7	12·4
Bedded	11·0	11·2	11·8

Difference necessary for significance 0·4 mm. (P=0·05.)

One-year-layered rootstocks in the larger size Grades were by now larger than corresponding bedded rootstocks, though originally smaller.

(*b*) *Height.*

The age of rootstock (i.e. one-year-layered and bedded) had no effect on the size of the maiden tree, and on the average poorly rooted stocks made as large trees as well rooted ones.

TABLE VII.

Average Maiden Height (cm.) of Pear Trees.

Amount of Rooting.	Original Grade of Stock Diameter.		
	1	2	3
Well aooted	64·8	70·7	74·2
Poorly rooted ..	69·9	67·7	70·4

Difference necessary for significance 2·3 cm. (P = 0·05.)

It was shown conclusively, however, that there were differences in height due to rootstock size, and that the degree of the difference was greater with well rooted than with poorly rooted stocks. (Table VII.)

PART III. THE INFLUENCE OF METHOD OF PROPAGATION AND OF VARIATIONS IN THE SCION SIZE AND VARIABILITY.

A. Comparison of Budded and Grafted Trees.

Apart from a few local varieties of plums which are sometimes grown on their own roots, two methods of fruit tree propagation are practised in Europe, namely, budding and grafting. Budding in July is the more common method and it is the practice of most nurserymen to graft in the following March (with the same scion variety) those stocks on which buds have failed. This mixture of methods may lead to higher variation and the following experiment, limited to apples, was designed as an attempt to find out the extent of differences in take, growth, size and variation in trees propagated by the two methods.

Material and Methods.

Material from two sources was available from which comparisons of the two methods could be made. The first of these covered the main experiment, while further comparisons in height and variation of one-year-old apple trees were possible on commercially raised trees.

The main experiment, which was carried out at East Malling, included Cox's Orange Pippin and Grenadier, on rootstocks Nos. I, II, IV, V, IX and XII. Each of the combinations, consisting of a single unit of 72 rootstocks, had been budded in August, 1937. In the following spring, to provide a comparison of

budded with grafted trees, each set was divided into four plots of 18 trees each. From two of these the buds were removed before they had started to grow and the rootstocks grafted with the variety with which they had originally been budded. The position of budded and grafted trees was, within each set, determined by chance, the arrangement of the four plots being either of the form GBBG or BGGB, where B indicates budded and G grafted trees.

Take was recorded in each combination and heights of all trees were measured weekly in half centimetres. From these records average heights and coefficients of variability were calculated.

On the average, budding gave a higher percentage take than grafting, the relative takes being 80% and 61% respectively. This, however, did not apply to all rootstocks, a somewhat better take resulting with grafts on rootstocks Nos. I, V and XII than on the others. Both Cox's Orange Pippin and Grenadier behaved similarly on each rootstock, but the differences between the two methods were slightly greater with the former variety.

TABLE VIII.

Average Heights (cm.) of Budded and Grafted Trees.

Variety and Rootstock.	Budded.	Grafted.
Cox's Orange Pippin on No. I.	124*	111
No. II.	119*	101
No. IV.	115†	90
No. V.	121†	103
No. IX.	104†	85
No. XII.	128†	90
Mean	119†	100
Grenadier on No. I	100	95
No. II.	96†	80
No. IV.	97†	80
No. V.	105*	96
No. IX.	81*	70
No. XII.	110*	98
Mean	98†	88

* Significant Difference, P=0·05.
† Significant Difference, P=0·01.

Height.

On the whole, budded trees made better growth by the end of the first season than grafted ones, as shown clearly in Table VIII. All differences, with the exception of Grenadier on No. I, were significant.

Variation.

It is clear from Table IX, that grafted trees were considerably more variable on the whole than budded ones. Cox's Orange Pippin on No. IV, and Grenadier

TABLE IX.

Coefficients of Variability for Budded and Grafted Trees.

Variety and Rootstock.	Budded.	Grafted.
Cox's Orange Pippin on No. I.	7·9*	14·5
No. II.	7·8†	22·1
No. IV.	9·2	20·0
No. V.	5·3†	20·9
No. IX.	7·2*	19·6
No. XII.	7·2†	21·5
Mean	7·7†	19·2
Grenadier on No. I.	12·1	12·7
No. II.	8·3†	19·3
No. IV...	12·1	20·2
No. V.	4·8†	12·2
No. IX.	13·9	21·1
No. XII.	8·8†	17·9
Mean	10·5†	16·7

* Significant Difference, P=0·05.
† Significant Difference, P=0·01.

on Nos. I, IV and IX did not show significant differences, though grafted trees always gave a higher coefficient of variability. Of the two varieties, Cox's Orange Pippin showed a larger difference between the budded and the grafted trees.

Comparison of Growth Curves.

Growth curves showing the average height each week of budded and grafted Cox's Orange Pippin are shown in Fig. 5.

There was little difference in the general form of the curves; growth of the grafted trees apparently fell off slightly more rapidly in the final seven weeks, particularly in Cox's Orange Pippin, and budded trees began growth earlier than grafted trees. This was to be expected since the union between bud and rootstock had already taken place by the time the trees were grafted. The curves for Grenadier were very similar to those for Cox's Orange Pippin.

The average weekly increment in growth for trees propagated by the two methods is illustrated in Fig. 6. These histograms show some differences between the growth of budded and of grafted trees. Although the grafted trees started later, their first flush of new growth was much more rapid than that of the budded trees. But it is also evident that the grafted trees of both varieties made their maximum weekly growth more than a month later than the budded trees. Furthermore, the effect of external factors (i.e. weather conditions, etc.) appears to have been less in grafted trees, since the deviations from normal were

less than in budded trees. Possible reasons for these deviations have been discussed in the first part of this paper.

Change in Variation during the Growing Season.

Curves showing the values of the coefficient of variability for height at the end of each week during the growing season are given in Fig. 7. In both varieties, the curves illustrated are those for rootstocks showing the smallest and the largest differences in variation.

It is clear that the variation of budded trees has always become stabilized earlier in the season than that of grafted trees. The differences in the times at

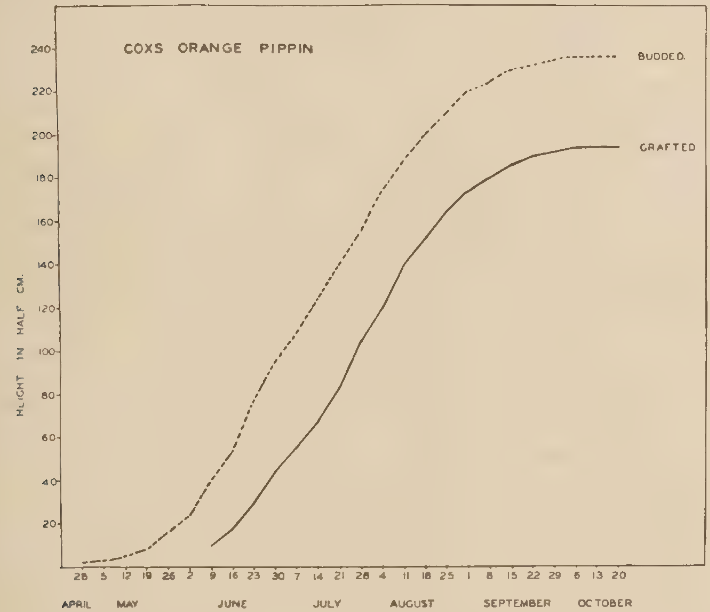


Fig. 5.

Growth curves comparing budded with grafted apple trees: Cox's Orange Pippin.

which this occurred varied and were not affected either by rootstock or by variety. It will be noted that the variability of budded Cox's Orange Pippin on No. V was greater on May 26th than a week previously. No explanation of this, however, was evident from the data.

Results in a Commercial Nursery.

The differences in size and variability between budded and grafted trees shown in this experimental nursery were confirmed by an examination of 1,528

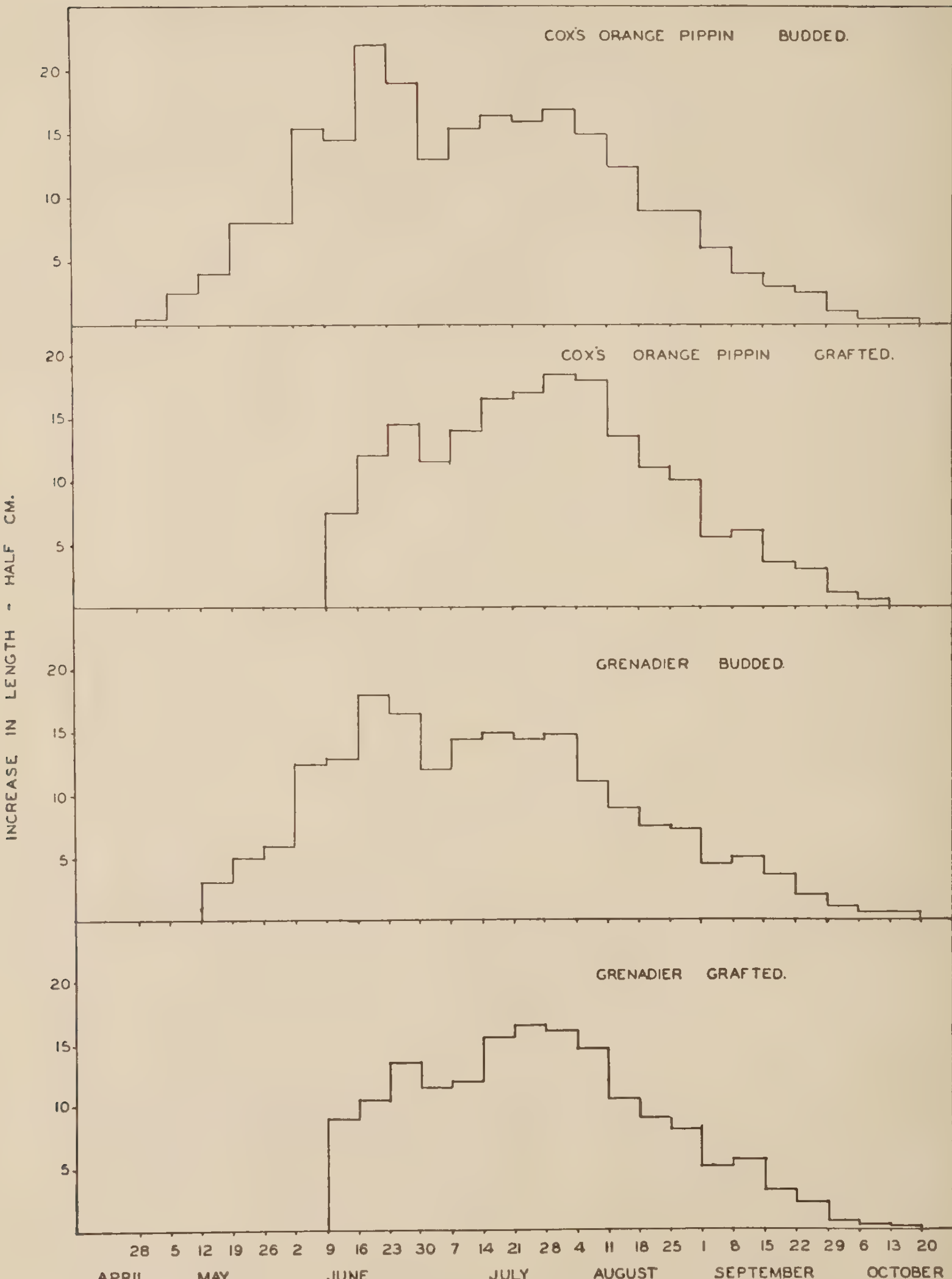


FIG. 6.

Weekly increments in growth for budded and grafted apple trees : Cox's Orange Pippin and Grenadier on six rootstocks.

budded and 2,250 grafted trees in a commercial nursery. Here there were four varieties of apple on rootstock No. XII and two on seedling Crab within which the comparison could be made. While all the trees were much more variable than

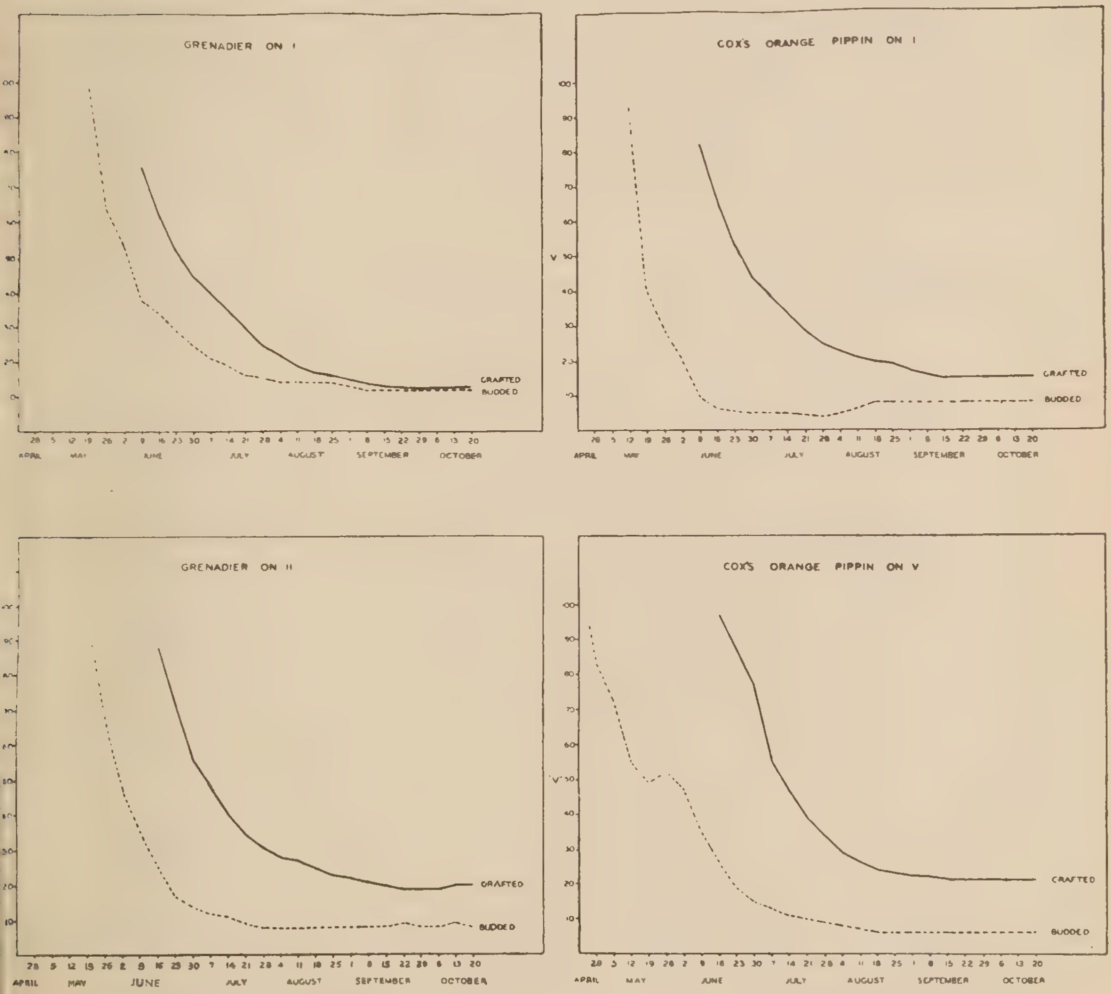


FIG. 7.

Curves showing the change in variation of budded and grafted apple trees; two varieties, each on two rootstocks.

those in the experimental nursery, in two instances, Cox on No. XII and Worcester on Crab, the grafted trees were significantly smaller and more variable; and in all the other varieties the budded trees were slightly larger and usually slightly less variable.

B. Influence of Kind of Bud and Method of Budding on Tree Variation.

In the propagation of fruit trees by budding the buds come from many sources. They may be from parent trees of differing ages and vigour and from various positions on the tree. The shoots from which the buds are taken generally vary greatly in size and therefore in the number of buds suitable for budding. In practice, all wood buds are used except those very close to the base of the shoots and those on less mature wood at the apical end, so that the buds have actually been formed at different times, those near the base being older than those towards the end. As the buds differ in the above characters, it seemed possible that these differences might affect the growth of the bud on the rootstock.

The orientation of the nursery rows varies in different plantations, so that some buds will receive more direct sunshine than others. It has already been demonstrated that the amount of sunshine does, to some extent, affect the growth of the bud. When the rootstock is cut back or " snagged " during the winter following budding, it is a common practice to leave about four inches of it above the bud to provide a natural stake to which the growing shoot is tied. This is removed later during the growing season. Some nurserymen, however, prefer to cut the rootstock immediately above the bud, thus avoiding a further cutting later in the season. On cutting the bud from the shoot bearing it a thin strip of wood is also removed. Most nurserymen in England remove this strip of wood from the bud-shield before insertion into the stock, but in North America the wood is left attached when budding apples and pears. Although most text-books, both English and American, state that no difference results from the two methods of preparing the bud, the only proof of this, to the writer's knowledge, is that given by Garner (1934).

To investigate the effects of the above factors on the size of the maiden tree, the following experiments were carried out :

1. *The Effect on Tree Size of Buds from Vigorous and from Weak Growing Shoots.*

This experiment was designed to find out whether buds from shoots of different sizes affect the take, size and variability of pears on clonal quince rootstocks. Although two workers (Crandall, 1918, and Halma, 1933) have shown that buds from shoots of different sizes when inserted on seedling rootstocks had no effect on tree size, this might not be so when possible differences due to the genetical make-up of seedling stocks are eliminated.

Material and Methods.

For this experiment, 240 Quince A rootstocks planted in a single row were budded in July 1937 with Conference and Durondeau pears. Buds from shoots

of two sizes were taken from a single parent tree of each variety. The shoots were first graded into five length-classes by eye and the middle class discarded, to avoid overlapping. Each shoot in the four remaining Grades was then measured. Before budding, the two large and the two small Grades were amalgamated, making one Grade of large and one of small shoots for each variety. The average lengths of shoots of Conference were 41 cm. and 26 cm., while those of Durondeau were 39 cm. and 25 cm. The only buds used were those from the central portion of shoots chosen at random from the required Grade. Each of the four combinations of variety and shoot size was duplicated in plots of 30 rootstocks.

Results.

There was practically no difference in take between buds from large and small shoots. Conference was slightly better than Durondeau, but the take in both varieties was reasonably good.

TABLE X.

Average Maiden Heights (cm.) for Buds from large and small Shoots.

Variety.	Size of Shoot.	
	Large.	Small.
Conference	84	84
Durondeau	76	81
Mean	80	82

Height.

No significant difference common to both varieties was observed, but whereas Conference showed no difference at all, the buds from small shoots of Durondeau gave significantly more growth. (Table X.)

In neither variety were the differences in variability found to be significant.

2. *Influence of Kind of Bud on Tree Size.*

The following experiment was designed as a further attempt to find out, in greater detail, whether buds from varying sources had a different influence on the growth of the maiden tree.

Material and Methods.

This experiment included two trials, Cox's Orange Pippin and Grenadier budded on rootstock No. I, and Conference and Durondeau pears on Quince A.

The apple and pear trials were designed to compare the effect of three and four factors, respectively, affecting the bud : (*a*) *Variety*. (*b*) *Age of parent tree*—in which buds from young and old trees were compared. (*c*) *Position of the bud on the tree*—buds from the outside as against those from the inside of the tree (pears only). (*d*) *Age of bud*—comparing early formed buds at the basal end of the shoot with those which were formed later, i.e. at the apical end. Thus, eight different kinds of apple and sixteen kinds of pear buds were compared.

Experimental Design.

Each experiment consisted of six randomized blocks, each containing two plots each of 40 rootstocks budded with a single variety.

Each of these plots was subdivided into eight sub-plots in the pear trial and four in that of apples. Thus, within each variety plot, the eight different kinds of pear buds were compared, using small plots of five rootstocks, and the four different kinds of apple bud in plots of ten rootstocks.

Source of Buds.

(*a*) Apples.

The parent trees, from which bud wood was selected, were 7 year-old and 17 year-old Cox's Orange Pippin and Grenadier, all on rootstock No. XVI. The young trees were non-bearing and had been cut back heavily each year to produce bud wood. Thus, the comparison of young and old trees was not a strict one ; nevertheless, a useful comparison was made of a common nursery practice and that of obtaining bud wood from established fruiting trees in the orchard.

(*b*) Pears.

Buds from 9 and 16 year-old trees of Conference and Durondeau, all on Quince A, were compared. Both sets of trees were bearing fruit.

Method of Selecting Bud Wood.

Two similar trees of each variety and age were selected in the spring of 1938. At the beginning of the season, when the buds which might make terminal shoots began growth, twenty on the outer branches and twenty towards the centre of each pear tree were labelled. With apples, thirty buds on outer branches of each tree were chosen. These were measured weekly throughout the growing season, so that shoots of similar growth might be selected for bud wood and shoots showing any irregularities in growth avoided. Twenty-four shoots were finally chosen from each pair of trees. The ranges in the size of shoots were as follows :—

Cox's Orange Pippin,	old	40-50 cm.
	young	42-57 cm.
Grenadier,	old	38-49 cm.
	young	47-61 cm.
Conference,	old	41-62 cm.
	young	35-67 cm.
Durondeau,	old	38-56 cm.
	young	30-62 cm.

It will be noted that as there were fewer shoots to choose from in the younger trees, those from these trees varied considerably more than those from older trees, particularly in the two pear varieties.

Each shoot supplied ten buds, five from the basal end and five from the apical end, avoiding buds from the extremes and as many as possible from the central portion of the shoot. At budding, the shoot from which buds were taken was chosen at random from each appropriate kind, with the exception that shoots from each tree of the pairs were used in different replications.

Results.

Records of take were made for each sub-plot and the heights of surviving trees were measured, as in previous experiments, at the end of August. No differences in take were apparent.

Height.

The effect on height differed somewhat for apples and pears, so that each is presented separately.

(*a*) Apples.

The only significant difference was that between the two varieties. Cox's Orange Pippin had an average height of 94 cm., while that of Grenadier was 65 cm.

Buds from bearing trees behaved in the same way as buds from non-bearing, rank-growing trees. The position of the bud on the shoot apparently had no effect on the size of maiden tree.

(*b*) Pears.

The analysis of the heights of two pear varieties on Quince A showed clearly that there were differences in each of the three comparisons. Durondeau made more growth than Conference, their average heights being 85 cm. and 74 cm. respectively. Table XI shows the average heights of the four combinations of age of parent tree and position of the bud on the shoot.

TABLE XI.

Average Heights (cm.) of Pear Trees.

Position of Bud on the shoot.	Age of Parent Tree.	
	Old.	Young.
Basal	76	79
Apical	79	84

Difference necessary for significance = 4 cm. (P = 0·05.)

On the average, buds from younger trees made better growth than those from older trees, the mean heights being 82 cm. and 75 cm. respectively. There was also a significant difference due to the position of the bud on the shoot, the mean height for buds from the apical end being 82 cm. while that for buds from the basal end was 77 cm. It is clear from the above Table that the difference in the effect of position of the bud on the shoot, though evident for both ages of parent tree, was significant only when the buds came from young trees. It is also seen that the effect of different ages of parent tree was significant only when the buds came from the apical end of the shoot.

Table XII shows the average heights for the four combinations of variety and age of parent tree.

TABLE XII.

Average Height (cm.) of Pear Trees.

Variety.	Age of Parent Tree.	
	Old.	Young.
Conference	74	74
Durondeau	81	89

Difference necessary for significance = 4 cm. (P = 0·05.)

Although there was, on the average, a difference in the effect of the age of parent tree on the growth of the bud, it is apparent that this difference occurred only with Durondeau.

The position of the shoot on the parent tree had no effect upon bud growth.

3. *Comparison of Different Manipulative Methods.*

Material and Methods.

Two trials were included in this experiment, Cox's Orange Pippin on rootstocks Nos. I and XII, and Conference pear on Quinces A and C. Both were

designed to compare rootstock effects and to make three comparisons of manipulative methods :—(*a*) *Position of the bud on the stock*—comparing North and South aspects ; (*b*) *Method of " snagging "*—comparison of trees snagged close to the bud before growth begins with those snagged four inches higher and cut back to the bud in the following August ; (*c*) *Preparation of the bud*—in which buds from which the wood in the shield had been removed were compared with those in which the wood was retained. Thus, eight different treatments were compared for each rootstock, making sixteen comparisons in each trial. The design of these trials was similar to that detailed on p. 24, the plots in the apple trial being replicated four times and in the pear trial six times.

Results.

(*a*) Apples.

The analysis showed, firstly, that maiden height was not affected by the rootstocks on which the trees were growing. However, snagging close to the bud resulted in larger trees. Table XIII shows the average heights of trees budded on the north and south sides of the stock, snagged high and snagged close to the bud.

TABLE XIII.

Average Height (cm.) of Apple Trees.

Aspect of Bud.	Method of Snagging.	
	Low.	High.
North	101	89
South	98	92

Difference necessary for significance=4 cm. (P=0·05.)

Although the difference between the two methods of snagging was significant for both positions of the bud on the stock, this difference was considerably greater where the buds were on the north side. Neither the aspect of the bud on the rootstock nor the removal of the wood from the bud had any direct effect on the size of apple trees.

(*b*) Pears.

Trees on Quince A made more growth than those on Quince C, their average heights being 79 cm. and 74 cm. respectively. Furthermore, snagging close to the bud, on the average, resulted in trees 79 cm. in height as against 74 cm. where the trees had been snagged six inches above. The degree of this effect

was shown to be related to the variety of rootstock and the aspect of the bud on the stock (Table XIV).

TABLE XIV.

Average Height (cm.) of Pear Trees.

Aspect of Bud.	On Quince A.		On Quince C.	
	Snagged Low.	Snagged High.	Snagged Low.	Snagged High.
North	85	74	76	72
South	80	79	76	73

Difference necessary for significance=4 cm. (P=0·05.)

Although snagging close to the bud resulted in larger trees, the differences were significant only where the bud was on the north side of the stock. Furthermore, the difference between the two methods of snagging was considerably larger with trees on Quince A.

In general, there was no great effect due to the removal of the wood from the bud-shield on the size of pear trees.

C. Influence of Kind of Graft and Method of Grafting on Tree Size.

Scions for grafting are usually obtained from all parts of the shoot, some being from the basal and others from the apical end. In grafting, it is common practice to make the sloping cut on the scion so that one bud is approximately mid-way between the top of the cut on the rootstock and the lower end of the scion. This results in varying positions of the top bud of the scion relative to the matched cambiums of rootstock and scion. In comparing effects of different positions of the top bud, workers have obtained conflicting results. It is usual with most nurserymen to pinch off, at the fifth leaf, growths other than that from the top bud, as it is believed that this will result in stouter one-year-old trees than by removing them completely, as is sometimes done.

These experiments were designed to investigate further the effects of the above treatments on the height of maiden apple and pear trees.

Material and Methods.

The experiment was carried out on Cox's Orange Pippin on one-year-layered rootstocks No. II, and was designed to compare the effects of three factors :—(*a*) *Portion of shoot selected for scion wood*—in which scions from the apical and basal ends of the shoot were compared ; (*b*) *Position of the top bud of the scion*—comparing grafts in which the top bud of the scion was directly above the matched cambiums of stock and scion with those in which it was above the mis-matched

side ; (c) *Treatment of side growths*—complete removal of growths other than that from the top bud as against stopping them at the fifth leaf.

Experimental Design.

The trial involved four randomized blocks each containing eight plots. These were in a single row, and to increase the accuracy of the experiment the method of "confounding" was employed (Yates, 1937). As the interaction of all three factors was likely to be unimportant, the plots in each block were arranged so that in the analysis of variance the effect of this interaction became inseparable from that due to position. This gave, in effect, eight smaller blocks of four plots each, the position of which was determined by chance in each replication. The size of each plot was increased to twelve trees, to lessen the effect of gaps, caused by graft failures, which had been rather large in the small plots (5 trees) used previously.

Source and Treatment of Scions.

The shoots from which the scions were cut were selected from eight seventeen-year-old Cox's Orange Pippin trees on rootstock No. XVI. The scions were grafted by the writer in the spring of 1939 using only those from a single tree in each block. These were cut from each end of the shoot, avoiding the extremes and its central portion. Each scion had four buds above the upper end of the sloping cut.

Growths other than that from the top bud were treated in two ways. On half the scions, they were completely removed after growth had begun, and on the other half they were pinched off after five leaves had formed. All were examined weekly during the growing season and the appropriate treatments carried out.

Results.

Take. No differences in take were observed which could be associated with treatment. The take in all plots was good and gave an average of 97 per cent. over the whole experiment.

Height. The analysis of variance for height showed clearly that scions from the basal end of the shoot made more growth than those from the apical end, the mean heights being 86 cm. and 81 cm. respectively. There was no effect on the height of tree due to the position of the top bud relative to the matched cambiums, or to the treatment of growths other than that from the top bud.

Diameter of maiden trees. Trees from scions from the basal end of the shoot were stouter than those from the apical end, their diameters being 9·2 mm. and 8·6 mm. respectively. There was also a significant difference due

to the treatment of side-growths, the mean diameter of trees from which these growths were completely removed being 8·5 mm., as compared with 9·3 mm. for those from which the growths had been pinched off at the fifth leaf. No effect was observed due to different positions of the top bud relative to the matched cambiums. This last result is in disagreement with the results of Roberts (1927), and of Swarbrick (1930), but confirms those of Bennett (1926), all of which were obtained with trees on seedling rootstocks.

GENERAL CONCLUSIONS.

In the three parts of this paper attempts made to determine the causes of variation in one-year-old fruit trees in the nursery are described. Although there is evidence that both the take of buds and the height of the one-year-old tree do vary from year to year, the period reviewed was too short to enable this to be ascribed to any particular set of climatic conditions. But sunshine and temperature influenced growth in the course of the growing season. Some varieties, and trees worked on certain rootstocks, vary more than others.

There is a tendency for all nursery trees to be very variable at the beginning of the growing season, but to level up greatly by the end of the main growth period.

On the whole, it would seem that, so far as *clonal rootstocks* are concerned, little advantage is to be gained, from the point of view of obtaining greater uniformity of material, by a closer grading for size or root development than is usual in good commercial practice. Indeed, bedded rootstocks, although larger and better rooted, gave trees no taller than those from one-year-layered rootstocks straight from the stools.

In a direct comparison, budded apple trees were shown to be, on the whole, larger and less variable than grafted ones. A contributing cause of this result may be the fact, shown in further experiments, that, whereas none of the differences in source of apple buds showed any effect, there was a clear difference due to the use of graft-wood taken from the basal as compared with that from the apical end of the shoot.

In one variety of pear, Durondeau, the position of the bud on the shoot and the age of the trees from which the shoots were taken did have some effect on budded trees, but in Conference no clear differences were observed.

Of the different manipulative methods examined, only the process of high snagging appeared likely to influence variation, and this only if buds were inserted in positions of variable aspect. Trees wherein the bud was placed in such a position as to be shaded by the snag were definitely smaller than those wherein the bud was placed in full sunlight. The removal or retention of the small piece of the wood in the bud-shield had no clear effect ; nor, in grafted trees, was there

any apparent influence of the position of the top bud of the scion in relation to the matched cambiums.

Finally, it is noteworthy that in nearly every comparison made, the larger trees were less variable for their size than the smaller. The trees in the nurseries in which best growth was made were also the most uniform. The nursery in which the exact experiments reported on in Part III were carried out was a particularly good one, and it seems possible that under less favourable growing conditions, some of the differences due to the various treatments might have been more marked. It seems likely, therefore, that with nursery trees on clonal rootstocks, if the general conditions conform to the best nursery practice, closer grading of the rootstocks and more careful selection of scions than is usual would hardly repay the extra labour involved.

ACKNOWLEDGMENTS.

The writer is indebted to Dr. R. G. Hatton of the East Malling Research Station under whose direction these studies were carried out, and to Mr. T. N. Hoblyn for much valuable advice and criticism. Thanks are also due to Mr. R. J. Garner for assistance in practical work and to the Pomology Section for help with recording.

SUMMARY.

PART I.

A study of the one-year growth of different varieties of apple and pear on a series of clonal rootstocks in four successive years showed that some varieties and rootstocks influenced variation more than others. Trees were more variable at the beginning of the growing season, owing to different times of bud-break, but levelled up after the growth peak. Pears were generally more variable than apples.

Though the trees as a whole were more variable in two out of the four seasons, the experimental period was not long enough to reveal the particular set of weather conditions most favourable to good and even growth. Weekly measurements in one season, however, showed that temperature and sunshine were more clearly associated with growth increments than soil moisture.

The more subject to good growth conditions the less variable were the young trees.

PART II.

The range in size and rooting of rootstock shoots on the stool was studied—the largest tending to be best rooted.

Rootstocks bedded out for a year before replanting and budding became larger and better rooted than rootstocks taken straight from the stool, but they

did not produce larger trees, since the latter rapidly caught up the former before the budding season.

With apple trees there was little evidence that size, age or rooting of the rootstock had any influence on the growth of the maiden tree. Larger pear trees resulted from the use of larger and better rooted quince rootstocks.

Part III.

Budded apple trees proved superior to grafted trees in take, size and uniformity. They also tended to start growth and to level up earlier in the season. In the first few weeks of growth, grafted trees grew more rapidly, but reached their growth peak approximately a month later than budded trees. After this, however, growth fell off more rapidly.

The source of the bud had no influence on the size of one-year-old apple trees.

Pear buds from young parent trees made more growth than those from older trees.

Larger pear trees resulted when the buds were taken from the apical end of the shoot, particularly when the shoots came from a young tree.

There was no apparent difference between pear buds from shoots which had originated from the more shaded branches and those from the outside of the parent tree.

When the rootstock stem was cut back close above the union in the spring (low snagging), the resultant trees were larger than those on which a snag four inches long was left until late summer (high snagging). This effect was accentuated when the bud was on the shaded side of the stock. Thus, unless all buds are inserted with exactly the same aspect, high snagging may lead to a greater variation in tree size.

There was no apparent advantage in removing the wood from the bud-shield before insertion.

Although, when budding apples, the origin of the bud was of no importance, when grafting them, scions from the basal end of the shoot made more growth than those from the apical end.

Stouter trees were obtained when side growths on grafted trees were allowed to make some growth and were pinched off at the fifth leaf.

There appeared to be no advantage in grafting in such a way that the top bud of the scion was directly in line with the matched cambiums of scion and stock.

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THE INFLUENCE OF EARLY TIMES OF FRUIT REMOVAL ON THE GROWTH AND COMPOSITION OF ALTERNATE-BEARING SUGAR PRUNE TREES WITH SPECIAL REFERENCE TO BLOSSOM BUD FORMATION*

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INTRODUCTION.

THINNING has long been practised to improve the commercial qualities of fruit, but only within recent years has it been modified so as to cause blossom buds to be formed in the fruiting year of biennial bearing trees. Magness and Overley (34) and Haller and Magness (19) first indicated that thinning apples heavily, so as to provide a comparatively large leaf area per fruit, would tend to cause annual blossoming. Then Aldrich (1, 2, 3), Harley (22) and Magness (35), and their associates, by adopting this practice and introducing earlier times of thinning, established annual blossoming in field trials with biennial bearing varieties of apples and pears.

Since 1935, Davis in unpublished work, has found very early and heavy thinning to bring about blossom bud formation in the fruiting or on-year in Sugar Prune trees at the Agricultural Experiment Station, Davis, California.

These experiments indicate that there is a critical time in the determination of blossom bud formation which is much in advance of that at which such buds can be distinguished with the aid of the microscope. In the Sugar Prune the critical time is about 35 days after full bloom, whereas according to Raglan (45) the floral primordia are not distinguishable till about 90 days after full bloom. If an excessive crop of young fruit remains on the trees after the critical time, even if it is subsequently removed, the formation of blossom buds is prevented.

The problem in the present investigation was to find what differences in

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growth and in composition were brought about by fruit thinning at different times which would account for this 35-day period being a critical one for blossom bud formation.

In presentation, the work falls naturally into four parts:

I. Seasonal growth, particularly of leaves, relative to the incidence of the critical time.

II. Quantitative differences in leaf and shoot growth relative to blossom bud formation.

III. Differences in chemical composition, also relative to blossom bud formation.

IV. Growth of the fruit, relative to the critical time and to the differences in growth and composition.

MATERIALS AND TREATMENTS.

Materials. The Sugar Prune trees used were growing on the University Farm Orchard, Davis, Califormia. Apart from those affected by thinning, they were in the complete alternate or biennial cropping condition, some being in their on- or bearing year and others in their off-, non-bearing year. They were irrigated on June 8th-10th, July 29th-30th, and September 10th to maintain available water (i.e. moisture between wilting point and the field capacity of the soils).

Treatments. The trees under investigation consisted of one fruiting tree in its on-year (F), one in its off-year (NB), and four other on-year trees (A, B, C, D) which were completely deblossomed or defruited by hand, each at a different time.

The times of fruit removal were determined as a result of previous experience and were so chosen that some trees were defruited before and others after the critical time for blossom bud formation. Tree A was deblossomed four days previous to full bloom (which was March 12th, 1936); B, 16 days, C, 30 days and D, 47 days after full bloom. The blossoming responses to these treatments in the following spring were: A, 100%, B and C, 75-100%, and D, 2-5%. These blossom estimates were kindly furnished by Dr. Davis.

In the present experimental treatment all the fruit was removed to obviate problems in sampling, although in previous experiments Dr. Davis had found that heavy thinning had given blossoming responses similar to those caused by complete fruit removal. One whole tree was devoted to each treatment, so as to provide abundant material for the many samples that were taken, without unduly depleting it of its shoots. Previous experience of the uniform response of these trees to deblossoming and defruiting indicated that single tree treatments would afford valid comparisons, and the present results have confirmed this view.

PART I.

Seasonal Growth relative to the Critical Time.*

To find the incidence of the critical time in the seasonal growth, observations were made on the time of growth in length and diameter of shoots, and a detailed study was carried out on leaf development. From scattered information some estimate could be formed beforehand of the short seasonal growth of spurs (47, 6), the somewhat longer growing season of leaves (28, 41, 48), the lengthy season of growth of terminal shoots (6) and of diametral growth (44) of apple varieties. There were no comparable data for the Sugar Prune or the plum.

Method.

Weekly samples of approximately 100 spurs were collected from the trees, to find the modal leaf number. Thirty spurs of the modal class, and finally six leaf-bearing spurs were taken, and the area of each leaf, from the proximal to the distal positions, was measured by a planimeter.

To check the accuracy of this method for obtaining an average seasonal development of leaf area, additional samples were collected from the fruiting tree, F, on March 28th and April 9th. The leaves (minus petiole) were weighed. The leaf area was determined (by planimeter) on a known weight of each sample, and from this an average leaf area per spur was calculated. The results are shown at points X and Y in Fig. 2, and demonstrate a close agreement between the values obtained by this weighing method and the planimeter measurements of the modal class.

Seasonal Growth of Spurs.

The central roll of leaves, which appears after the breaking of the buds and the abscission of the bud scales and of some transitional foliar organs, opens rapidly ; the number of leaves is established early and further primary growth of the shoot is limited by the death and abscission of its tip. By three days after full bloom, three leaves had generally separated from the central roll, and by eight days all leaves had unfolded in most of the four- and five-leaved spurs. By 27 days the internodal growth of the spurs had apparently ceased and the petioles showed a joint at their insertion on the shoot. By 37 days after full bloom, only spurs with 8 or more leaves were capable of increasing in leaf number, as the terminal point was dead and abscissing from the shorter spurs with fewer leaves. At their insertion the petioles were more swollen and axillary buds were appearing. Spur growth in length had ceased, but radial thickening took place subsequently.

* Re-written from part of the Author's M.S. Thesis (7).

The increase in the average number of leaves per spur is shown in Fig. 1. The average per spur of F did not increase after March 20th, 8 days after full bloom; of B and C after April 2nd, 21 days after full bloom; of A after April 7th, 26 days after full bloom. There are two inconsistencies in these data: first, the anomalous position of C which from more extensive data obtained later was found to give a lower average number of leaves than B; secondly, since B and C carried fruit for 16 days and 30 days, respectively, the average number of leaves of F also should have coincided with those treatments for the time they carried fruit.

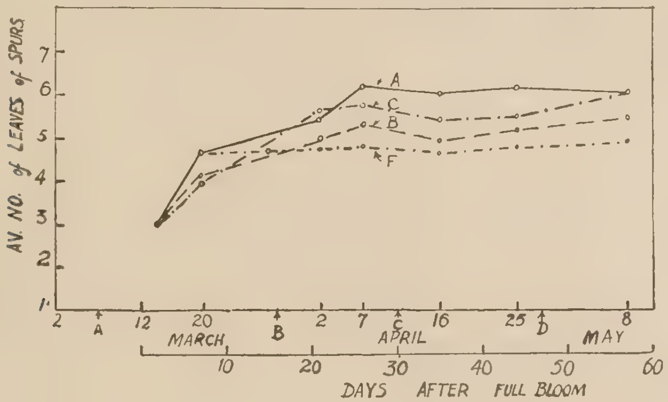

Fig. 1.
Seasonal increase in leaf number of spurs.

Seasonal Expansion of Spur Leaf Area.

The data for the seasonal expansion of spur leaf area are given in Fig. 2. Up to April 7th, 26 days after full bloom, the leaf area expanded at a uniform rate for all treatments, and this appears as a single line in Fig. 2.

At this time, the rate of leaf growth increased, and at a different rate for each treatment, so that the different treatments showed different leaf areas by April 16th. The subsequent expansion of leaf areas was comparatively small and gradual in A, B and C and negligible in F.

The most important period in the leaf growth of spurs was from 26 to 35 days after full bloom. At this time differences in leaf area became manifest regardless of whether flowers had been removed from the trees 30 days before or fruit had been removed 14 days before or even 4 days after the onset of this period. These differences were caused by the differential growth of leaves 4, 5 and 6 of the spurs.

The development of individual leaves for the extreme treatments A and F, shown in Fig. 5 (*a*) and (*b*), was similar in all treatments up to April 7th and thus gave the single line in Fig. 2. By this time leaves 1 and 2 had ceased

growth and leaf 3 was approaching cessation of growth; but leaves 4, 5 and 6 started to expand rapidly and caused the distinct change in the growth rate and the final differences in the total leaf area. The greatest expansion in leaf area, that of the fifth and sixth leaves, appeared after the cessation of growth in length of the great majority of the spurs, which was shortly before the observation was made that the tip of the spur was dead and abscissing, on April 16th.

The increasing size of leaves in their acropetal succession is also of interest as reflecting the favourableness of conditions for leaf growth. The early leaves were small, indicating that conditions at that time were not favourable to leaf development. Among these, the facts that numbers of distal leaves were in the early stages of growth and many shoots were in active growth, are probably the

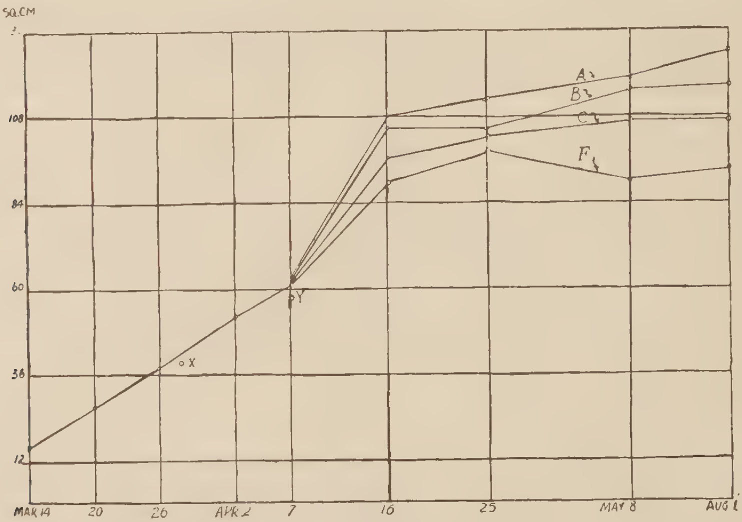

FIG. 2.
Seasonal expansion of leaf area of six-leaved spurs of trees A. B. C and F.

most important. The load of fruit does not appear to be important at this time, as corresponding leaves in the different treatments were identical in area for a period of 26 days. After this time conditions for leaf growth must have improved, probably because competition from shoot growth was much reduced, as the later leaves expanded more rapidly than the earlier ones and reached a much larger size.

Incidence of the Critical Time.

The seasonal expansion of individual leaves, among themselves and also in relation to the other developments of the shoot, presented a remarkable example of correlated growth. Earliest of all came the establishment of the number of

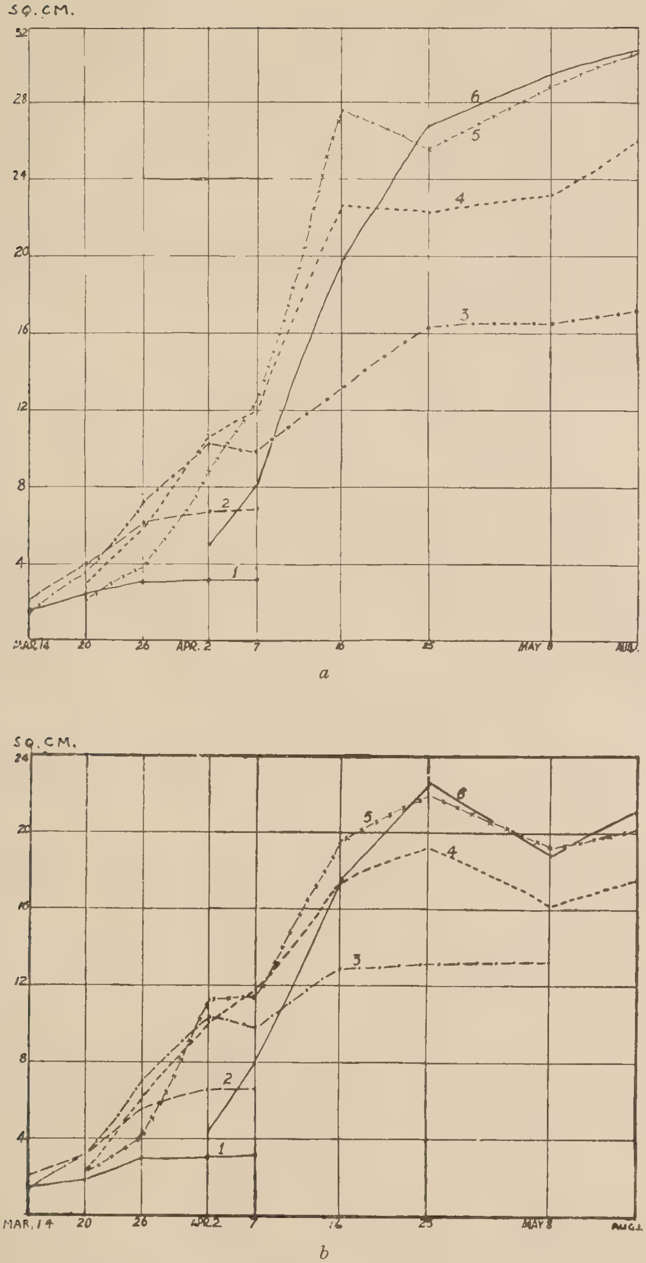

FIG. 3.

Growth of individual leaves of six-leaved spurs of (*a*) tree A, and (*b*) tree F. The leaves are numbered from proximal to distal positions.

leaves (leaf number), then internodal growth in length and cessation of this growth in the spurs, followed by the expansion of distal leaves and, lastly, by the diametral growth of the spurs.

The critical period occurred at the time of expansion of the distal spur leaves ; where this was vigorous, as in A, B and C, blossom buds formed again that season. In attempting to interpret these data for the leaf growth of the tree as a whole, later findings should be considered, namely, that the mean leaf number per shoot was A, 7·5 ; B, 7·3 ; C, 6·2 ; D, 5·4 and F, 4·8. The differences in the leaf expansion proceeding at the critical time were, therefore, much greater than those represented by the leaf growth of six-leaved spurs.

PART II.

Mean Shoot and Leaf Growth.

The literature affords very little indication of what differences in shoot length and leaf area might be expected from thinning at a series of times after full bloom. Thinning at the usual time does not generally increase leaf area and shoot length (8, 37, 18, 17, 53), but removing the blossoms has been shown (41, 48, 9, 46) to increase the leaf area.

Shoot growth has been extensively investigated for its relation to blossom bud formation. Regularly bearing apple trees, whether of annual or biennial varieties, have been shown (55, 46, 23, 5, 36) to present a marked and positive correlation between blossom bud formation and length and diameter of the spurs.

In biennial trees this correlation is nullified, the heavy crop preventing blossom bud formation, irrespective of the length of shoot growth. Roberts (46, 47) and other workers found that the average growth was less in the on-year, and this led him to suggest that shoots did not grow enough in length and diameter to form blossom buds in that year ; but the further investigations of Mack (33) and of Tucker and Potter (49) indicated that the growth made in the on-year may be greater than that in the off-year, and Mecartney (36) and others pointed out that blossom buds are absent in the on-year on lengths on which they would be formed in the off-year. A quantitative relationship between growth and blossom bud formation is therefore not clear.

Method.

The methods employed in measuring growth that appear in the literature show great diversity and a lack of comprehensiveness in assessing its amount. Among the measurements used are the following :—

(*a*) The annual extension in length of the shoots, either of the entire range, or of only some of them, such as the terminals or the spurs. Of the spurs, the different kinds of primary or secondary growths may have been examined separately or not.

(*b*) The leaf numbers and areas per spur or an average leaf area.

(*c*) The diametral growth of either spurs, shoots and branches or of the trunk.

(*d*) Dry weight determinations of the plant parts or of the entire plant.

The difficulty with all single measurements except (*d*) is that they lack comprehensiveness. Hoblyn (26) and Wilcox (54) have both pointed out the inadequacy of any single measurement, but decided that trunk circumference was probably the most satisfactory single one for field experiments.

From the viewpoint of plant physiology the best and final measurement of plant growth is the dry weight. To determine this, however, is out of the question in many field experiments, although Chandler (9) used it to obtain the most conclusive data that are available on the influence of fruiting on growth. Doubtless dry weight could be used more widely, yet separate values for growth in length, foliage and diametral growth are desirable, as in the present experiment, because many of the existing data are expressed in these terms. Nevertheless they should be expressed in some comprehensive manner, and this was accomplished by developing a method of using relative values.

Frequency Distributions.

Vyvyan and Evans (52) made a morphological analysis of the leaf area of two entire apple trees and found that it was necessary to divide the leaf-bearing shoots into a number of classes, viz. :—

1. primary leaf shoots ;
2. primary leaf spurs ;
3. primary blossom spurs (cluster bases) ;
4. secondary growths (*a*) spurs and shoots ;
   (*b*) axillary spurs and shoots.

Each class had its own frequency distribution and this should be measured separately to reach an evaluation of the leaf area of a tree.

In the Sugar Prune, however, the shoots are all primary (whether they blossom or not) there being no secondary shoots arising from primary blossoming spurs, as in the apple. Further, it was discovered in the early samples that the shoots of all lengths form a frequency distribution with a single mode. Spurs and

longer shoots thus comprise a single population in the Sugar Prune, not two groups as Vyvyan and Evans reported for the apple, and it would be inaccurate to measure separately any part of the population such as the spurs or the laterals.

The frequency distribution of the prune shoots is of Pearson type I (*a*) (38). The significance of this type of distribution is that, although the standard deviation could be calculated, it could not be used to provide a standard or probable error, as the curve from which it would have been derived was not Gaussian. Hence the means of the leaf and shoot measurements were calculated, but the significance of difference between means was not estimated. However, the treatments were planned to form a series and they gave a seried growth response, which can clearly be set out in relation to the critical time for blossom bud formation (see Fig. 4).

The significance of the type of distribution in fruit trees has not received previous attention although several workers (46, 36, 15, 43) have presented either frequency curves or tables which show it.

Growth Measurements Recorded.

Shoot lengths and leaf numbers were recorded in June, 1936, on units of entire limbs of the trees. They were made on every shoot in turn, so that the leaf number corresponding with each length measurement is known.

The records were taken on more than one limb for most treatments ; a comparison of the several means thus affords a measure of the reliability of the general mean. This comparison for the mean shoot lengths of several limbs is shown in Table I.

TABLE I.

Comparison of the Mean Shoot Lengths of Several Limbs.

Treatment.	1st Limb.		2nd Limb.		3rd Limb.		4th Limb.		Totals.	
	n.	m.	n.	m.	n.	m.	n.	m.	n.	m.
A	745	4·74	297	4·69	—	—	—	—	1,042	4·71
B	578	3·98	591	4·31	449	3·97	—	—	1,619	4·07
C	463	2·14	437	2·75	351	2·22	546	2·51	1,797	2·31
D	1,115	1·55	—	—	—	—	—	—	1,115	1·55
F	512	0·808	588	0·697	—	—	—	—	1,100	0·75
NB	938	1·225	—	—	—	—	—	—	938	1·22

n = number of shoots. m = mean.

When the values for length and leaf number were sorted into frequency distributions, they at once showed extremely skewed or J-shaped distributions, with a single mode, which was in the spur classes. A further sample of about 200 shoots (more than 10 cm. in length) was measured on other limbs in most

treatments, to ascertain from a larger sample if long shoots (laterals) formed a second mode and would thus give a bimodal curve for length and leaf number, as Vyvyan and Evans had described for leaves. To obtain these additional shoot samples, the procedure was to measure all shoots 10 cm. long and longer on limb after limb around the tree, until approximately 200 measurements had been taken on these several entire limbs. The frequency distributions of these shoots revealed no second mode and confirmed the expectation that they comprised the tail of a very skewed, J-shaped, curve.

Leaf area per shoot was determined for each treatment from a random sample of about 200 shoots collected in late July and brought into the laboratory, where the total leaf area for each shoot was measured by a planimeter, used in a stardardised way. The instrument was checked periodically against a standard area, and an error of 2 per cent. was found for repeated measurements of a leaf area of 100 square centimetres.

An average area per leaf was determined from the above sample of 200 shoots.

Diameter measurements were made on a random sample of 100-150 spurs brought into the laboratory and measured by calipers. Two samples were taken—one for May and the other in June. The June sample was regarded as the one in which the treatments would show their final differences.

Presentation of Data.

Number of Leaves per Shoot.

Fruit removal at progressively later times in the season caused a graded decrease in the mean leaf numbers, as follows :—A, 7·5; B, 7·3 ; C, 6·2 ; D, 5·4 F, 4·8, and NB, 4·7.

The frequency distributions are set out by class intervals of 5 leaves in Table II ; those of the first three classes are given in detail in Table III ; and those of additional shoots appear in Table IV. The frequency distributions of leaf number per shoot are extremely skewed and have single modes. Shoots of all lengths thus form a single population, but, to aid an analysis of the differences between the treatments, the shoots with 10 leaves and less will be called spurs and those with more leaves, laterals. The number of laterals is given as a percentage of the sample in Table II.

Fruit removal at different times altered the frequency distributions in a quite definite manner. The fruiting tree had a modal class of 5 leaves per shoot and only 0·5 per cent. laterals. None of the laterals exceeded 15 leaves per shoot. Fruit removal at 47 days (D) was done too late to affect the distribution in the spur classes, but it increased the number of laterals (3·0 per cent.,) Fruit removal at 30 days (C) gave the same modal class as D and F, namely 5

leaves per shoot, but it caused increase in the classes immediately succeeding the modal class, an appreciable increase in the laterals (5·9 per cent.), and the laterals extended to higher leaf numbers than D. Fruit removal at 16 days (B) raised the modal class to 6 leaves per shoot and increased still further the frequencies in the classes immediately succeeding the modal class and also raised the number of laterals (8·7 per cent.). This was effected by increasing the frequencies in the various lateral classes, without increasing the range of the classes, which is similar to C. Blossom removal (A) gave a modal class of 6 leaves, like B, but gave higher frequencies than B in the succeeding classes (up to 20 leaves per shoot) and lower ones in the still higher classes. A showed fewer laterals than B (3·3 per cent.).

TABLE II.

Frequency Distribution of Leaf Numbers per shoot.

Classes.. ..	A.	B.	C.	D.	F.	NB.
1- 5 leaves ..	377	518	1,020	840	818	806
6-10 ,, ..	530	531	671	240	276	108
11-15 ,, ..	67	39	21	18	6	7
16-20 ,, ..	29	22	22	3	—	9
21-25 ,, ..	21	26	16	6	—	6
26-30 ,, ..	10	13	17	8	—	—
31-35 ,, ..	8	9	5	—	—	1
36-40 ,, ..	—	8	2	—	—	1
41-45 ,, ..	—	2	4	—	—	—
46-50 ,, ..	—	2	1	—	—	—
N.=	1,042	1,170	1,797	1,115	1,100	938
M.=	7·5	7·3	6·2	5·4	4·8	4·7
Laterals % ..	3·3	8·7	5·9	3·0	0·5	2·6

The earlier times of fruit removal thus altered the frequency distributions in the following ways :—

(1) Shifted the mode to a higher class.

(2) Increased the frequencies of the classes immediately following the modal class.

(3) Progressively increased the percentage of laterals.

(4) Increased the range of classes of laterals, except that A was less than B.

The off-year tree (NB) had a characteristic kind of growth. It resembled the fruiting tree in the spur classes but had 2·6 per cent. laterals, similar to D. This tree threw out a number of small spurs on the older wood of the spur clusters, which increased its number of growing points by 30 per cent. over the number in the trees that blossomed.

TABLE III.

Frequency Distribution of Leaf Numbers per shoot.

(Shoots with 1-15 leaves.)

Classes	A.	B.	C.	D.	F.	NB.
2 leaves ..	9	11	15	18	18	47
3 ,, ...	75	84	144	136	141	154
4 ,, ...	140	120	304	357	305	287
5 ,, ...	153	303	557	329	354	318
6 ,, ...	214	337	453	156	174	73
7 ,, ...	166	129	125	41	73	20
8 ,, ...	79	39	48	32	20	8
9 ,, ...	45	16	25	15	6	5
10 ,, ...	26	10	19	6	3	2
11 ,, ...	16	14	3	7	3	—
12 ,, ...	21	12	6	3	2	2
13 ,, ...	9	5	6	3	1	2
14 ,, ...	11	2	2	4	—	2
15 ,, ...	10	6	4	1	—	1
N. = ...	974	1,088	1,712	1,098	1,100	921

TABLE IV.

Frequency Distributions of Leaf Numbers per shoot (of additional shoots with more than 10 *leaves per shoot).*

Classes ..	A.	B.	C.	NB.
11-15 leaves ..	135	50	26	85
16-20 ,, ..	63	48	38	47
21-25 ,, ..	27	48	16	34
26-30 ,, ..	17	14	12	29
31-35 ,, ..	12	27	5	12
36-40 ,, ..	5	11	2	5
41-45 ,, ..	2	5	1	3
46-50 ,, ..	1	7	2	6
51-55 ,, ..	1	4	2	4
56-60 ,, ..	2	4	—	—
61-65 ,, ..	0	—	—	—
66-70 ,, ..	1	—	—	—
N. =	266	218	104	225

Length of Shoots.

The average length of the shoots produced by the fruit removal treatments was as follows :—A, 4·71 cm. ; B, 4·07 cm. ; C, 2·31 cm. ; D, 1.55 cm. ; F, 0·75 cm. ; and NB, 1·22 cm. The difference between D, F and NB was due to the laterals, as the average length of the spurs was 0·75 cm., 0·75 cm., and 0·58 cm. respectively.

The frequency distributions of the shoot lengths are given in Tables V, VI, and VII, corresponding respectively with Tables II, III and IV of leaf number. Table V gives the distributions of the entire samples by class intervals of 5 cm.,

TABLE V.

Frequency Distribution of Shoot Lengths.

Classes (cm.)	A.	B.	C.	D.	F.	NB.
0·1- 5·0 ..	876	1,046	1,706	1,077	1,094	912
5·1- 10	52	29	10	15	6	4
10·1- 15	30	13	11	4	—	1
15·1- 20	16	9	15	1	—	6
20·1- 25	10	9	13	—	—	3
25·1- 30	13	12	5	2	—	3
30·1- 35	14	8	9	3	—	4
35·1- 40	4	7	6	1	—	—
40·1- 45	5	12	4	6	—	3
45·1- 50	2	5	3	1	—	1
50·1- 55	6	3	2	2	—	—
55·1- 60	5	1	3	1	—	—
60·1- 65	3	5	3	—	—	1
65·1- 70	1	1	1	1	—	—
70·1- 75	3	4	1	1	—	—
75·1- 80	1	1	1	—	—	—
80·1- 85	1	—	1	—	—	—
85·1- 90	—	3	1	—	—	—
90·1- 95	—	—	2	—	—	—
95·1-100	—	—	—	—	—	—
100·1-105	—	2	—	—	—	—
105·1-110	—	—	—	—	—	—
N. = ...	1,042	1,170	1,797	1,115	1,100	938
M. = ...	4·7	4·1	2·3	1·5	0·7	1·2
Means of spurs (0·1-10 cm.) ..	—	—	—	0·75	0·75	0·58
Laterals % ..	11·0	8·1	4·5	2·0	0·0	2·3

TABLE VI.

Frequency Distribution of Shoot Lengths (Shoots 0·1-5·0 cm. long).

Classes (cm.)	A.	B.	C.	D.	F.	NB.
0·1-0·5	312	447	877	780	776	788
0·6-1·0	325	405	548	212	188	74
1·1-1·5	97	94	140	36	75	25
1·6-2·0	53	48	59	19	25	8
2·1-2·5	36	—	28	7	—	—
2·6-3·0	17	32	25	9	21	9
3·1-3·5	—	—	7	4	—	—
3·6-4·0	26	14	11	6	6	4
4·1-4·5	—	—	2	—	—	—
4·6-5·0	10	6	9	4	3	4
N. = ...	876	1,046	1,706	1,077	1,094	912

TABLE VII.

Frequency Distribution of Shoot Lengths of Additional Shoots (more than 10 cm. long).

Classes (cm.).	A.	B	C.	NB
11- 15 ..	55	21	22	30
16- 20 ..	38	28	17	31
21- 25 ..	34	16	7	18
26- 30 ..	27	19	10	21
31- 35 ..	15	18	4	15
36- 40 ..	18	16	7	11
41- 45 ..	17	11	4	10
46- 50 ..	6	13	3	5
51- 55 ..	7	9	0	4
56- 60 ..	7	14	0	11
61- 65 ..	1	4	1	8
66- 70 ..	6	9	1	4
71- 75 ..	2	3	2	3
76- 80 ..	3	2	2	1
81- 85 ..	0	2	1	—
86- 90 ..	1	3	1	—
91- 95 ..	—	2	—	—
96-100 ..	—	2	—	—
101-105 ..	—	3	1	—
106-110 ..	—	1	—	—
111-115 ..	—	—	—	—
116-120 ..	—	1	—	—
121-125 ..	—	—	1	—
126-130 ..	—	—	—	—
131-135 ..	—	1	—	—
136-140 ..	—	1	—	—
No. = ..	240	199	84	174

Table VI the detailed distribution in the 0·1 to 5·0 cm. classes and Table VII the distribution of lengths in the additional samples of laterals. The frequency distributions are J-shaped, with single modes. The shoots 10 cm. and less in length are called spurs, those above 10 cm. are called laterals. The numbers of laterals are expressed as percentages of the entire samples in Table V. These percentages being on the basis of length, differ from those based on leaf number shown in the previous section.

Fruit removal had an effect on the frequency distributions of shoot lengths similar to that shown on leaf numbers.

Leaf Area of Shoots and Mean Leaf Area.

The average leaf areas of samples of about 200 shoots from the various fruit removal treatments are given in Table VIII.

As a basis for using these samples, it is first necessary to compare their average number of leaves with that of the large samples previously recorded. The values, shown in column five of Table VIII, agree closely, except that D and NB are high to the extent of about 10 per cent.

Treatments A and B show distinctly greater leaf areas of shoots than other treatments ; treatments F and NB show low areas ; C shows an area intermediate between these extremes ; D shows an increase in average area over F ; but since it will be shown later (relation of the number to the area of leaves) that the leaf areas of similar leaved spurs in D and F were similar, D is rather to be grouped with F and NB in the lower leaf area group. The increased area of D is almost solely due to laterals.

TABLE VIII.

Leaf Area of Shoots and Mean Leaf Area.

Treatment.	No. of shoots in sample.	No. of leaves measured.	Av. No. of leaves.	Difference from Mean No. of leaves given in Table V.	Leaf area per shoot. sq. cm.	Mean leaf area. sq. cm.
A.	200	1,523	7·6	+0·1	133·9	17·7
B.	193	1,370	7·1	−0·2	120·2	17·4
C.	192	1,250	6·5	+0·3	104·2	16·0
D.	198	1,181	6·0	+0·6	85·8	14·4
F.	200	936	4·7	−0·1	52·1	11·2
NB.	200	1,067	5·3	+0·6	64·9	12·2

TABLE IX.

Frequency Distribution of Leaf Areas of Shoots.

Classes (sq. cm.)	A.	B.	C.	Classes (sq. cm.).	D.	F.	NB.
				10- 29	33	54	49
				30- 49	28	50	52
20- 50	19	29	40	50- 69	53	51	44
51- 80	30	69	64	70- 89	18	23	14
81-110	45	45	40	90-109	31	8	13
111-140	43	17	18	110-129	3	9	8
141-170	25	8	7	130-149	11	—	7
171-200	9	—	2	150-169	4	3	1
201-230	5	3	6	170-189	1	—	1
231-260	3	10	2	190-209	3	2	1
261-290	3	4	5	210-229	3	—	1
291-320	3	1	3	230-249	2	—	3
321-350	7	3	3	250-269	1	—	1
351-380	2	1	—	270-289	3	—	1
381-410	2	—	1	290-309	—	—	2
411-440	—	1	—	310-329	2	—	1
441-470	2	1	—	330-349	—	—	1
471-500	1	1	—	350-369	—	—	—
501-530	1	—	1	370-389	—	—	—
				390-409	—	—	—
				410-429	1	—	—
				430-449	1	—	—
N. =	200	193	192	N. =	198	200	200
M. =	133·9	120·2	104·2	M. =	85·8	52·1	64·9

The frequency distributions of the leaf areas are given in Table 9. They are much skewed towards the low leaf area classes and have a single mode. Compared in the order A, B, C, D, F, they show, like length and leaf number, that the mode moved progressively to a higher leaf area class the earlier the fruit was removed from the tree.

The mean leaf areas, also given in Table VIII, show that A, B and C, give high values, F and NB low values, and D an intermediate value.

Spur Diameters.

The mean diameters of the spurs, given in Table X, indicate very little difference between the thinned trees and the fruiting trees by the end of the growing season, although the difference was probably significant in May. This similarity is more apparent than real, as the spurs of F were predominantly short and relatively stout, whilst those of A, B and C included more long ones. Long spurs are usually thinner than short ones, because the sub-axillary wedges coalesce in the latter but do not in the long spurs. Great differences appeared in the diameter of the long shoots.

TABLE X.

Mean Diameter of Spurs (cm.).

	A.	B.	C.	D.	F.	NB.
May 22nd	0·36	0·38	0·38	0·37	0·24	
July 30th	0·45	0·43	0·46	0·40	0·36	0·40

There was no difference between D, which did not form blossom buds, and A, B and C which did. This is contrary to the suggestions, particularly of Roberts (47), that diametral growth is an external criterion of the fruitful condition.

The reason for the similarity of A, B, C, and D is that the seasonal diametral growth of spurs takes place after the critical time and that of laterals still later. The laterals of both A and F were in the prominent axillary wedge stage in late April, six weeks after blossoming, and were similar in appearance; but by July 27th A had developed secondary thickening almost sufficient to obliterate the wedges, whilst F showed only slight secondary thickening so that the wedges still remained prominent. Fruiting inhibited diametral growth, as has previously been indicated for the apple (47, 26, 54), but only if the fruit was carried after 47 days (D), because the main increases in diameter were made after this time, when also, if the fruit was on the tree, it would make its demands on the food materials.

Discussion.

Mean Leaf and Shoot Growth in Relation to the Critical Time.

The different measurements of shoot and leaf growth that have been presented separately may now be considered together on a relative basis and in a more generalized form so as to show the effect of fruit removal on them as a whole. The mean values given previously have been converted to relative figures on the basis of the fruiting tree as 100. They appear in Table XI. The data are then used to show the relationship of growth to the critical time in Fig. 4, where they are plotted against the time when the fruit was removed.

Table XI.

The Relative Amounts of Leaf and Shoot Growth.

	Leaf No. per shoot.	Leaf area per shoot.	Length per shoot.	Diameter of spurs.	Area per leaf.
NB.	98	125	162	111	109
F.	100	100	100	100	100
D.	112	164	206	108	129
C.	129	210	308	122	143
B.	151	230	543	116	156
A.	155	257	629	120	159

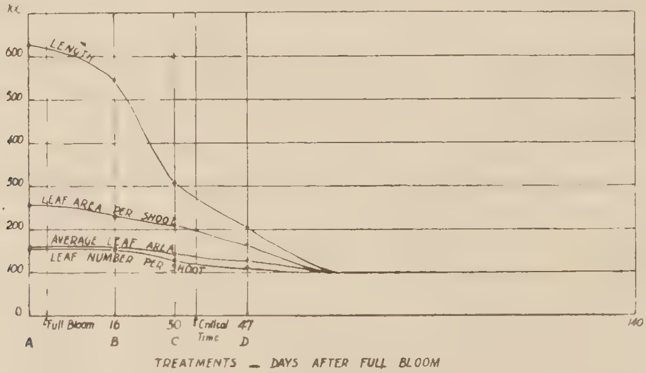

Fig. 4.

Relation of growth to the critical time for blossom bud formation.

These curves epitomize the growth data. They are reversely *sigmoid.* (Leaf area per shoot and per leaf would also appear sigmoid if plotted on an exaggerated vertical scale, and allowance made for the fact that the values for D are 10 per cent. high.)

The critical period for blossom bud formation, at about 35 days after full bloom, falls low in the steeply declining part of Part II of the sigmoid curves.

There is here a definite general relationship of growth to blossom bud formation, but particularly about the critical time the differences in growth were not critical. The relationship does clearly show that to bring about blossom bud formation again in the same year in on-year trees it is necessary to cause considerably greater growth than that which occurs in a fruiting tree. Fruit removal at six weeks (D), which did not cause blossom bud formation, had comparatively little influence on leaf and shoot growth.

The significance of the greater growth made by trees A, B, and C probably lies in the fact already shown in Part I that it would have been active at 35 days after full bloom, whereas trees D and F would have been making comparatively little growth at that time.

In the correlated seasonal growth of shoots and leaves, the critical time occurs after the cessation of growth in length of the spurs, and during the expansion of the distal spur leaves. The quantitative differences in leaf growth taking place at the critical time, as indicated in Part II by a consideration of the seasonal growth together with the mean leaf numbers, were large ; and, if the critical time is one of change in development (phasic growth) induced by growth substances produced by the leaves, then the significance of the differences in growth among the trees and the reason why there is a *time* which is critical, becomes apparent.

Such an hypothesis can readily be seen to satisfy variations of blossom responses met with in the field. It satisfies variations in the critical time among varieties, between localities and between trees of different vigour in one locality, because different seasonal and nutritional conditions affect the vigour or growth of the shoots and leaves. It also fits in with the well established correlation between blossom bud formation and vigour in annual bearing trees. Only the more vigorous spurs can maintain leaf growth in the presence of a crop after the critical time or phase, and thus induce later blossom bud formation. This places the production and functioning of a growth substance on an individual spur basis.

The complete loss of spur individuality in biennial trees occurs when, in the on-year, cropping imposes a check on even the more vigorous spurs and prevents the accomplishment of the ripeness to blossom phase. In an off-year tree, blossom bud differentiation in the smallest spurs is probably due to the translocation of a growth substance, as such spurs are generally in a proximal situation to more vigorous growth.

DERIVED DATA.

In the data already presented all measurements were affected by the treatments. Length was affected most, leaf area less and leaf number per shoot least. These results indicate that early times of fruit removal gave a much greater leaf area and especially length per shoot than would be expected from the increase

in leaf number per shoot. They also illustrate the physiological dependence of shoot length on leaf area and of area on leaf number.

Both shoot length and leaf area can, however, be related to a common constant basis, namely leaf number.

Relation of Number to the Area of Leaves per Shoot.

The average leaf area for each leaf number class was calculated and is given in Fig. 5. It shows that the time of fruit removal affected the leaf area produced

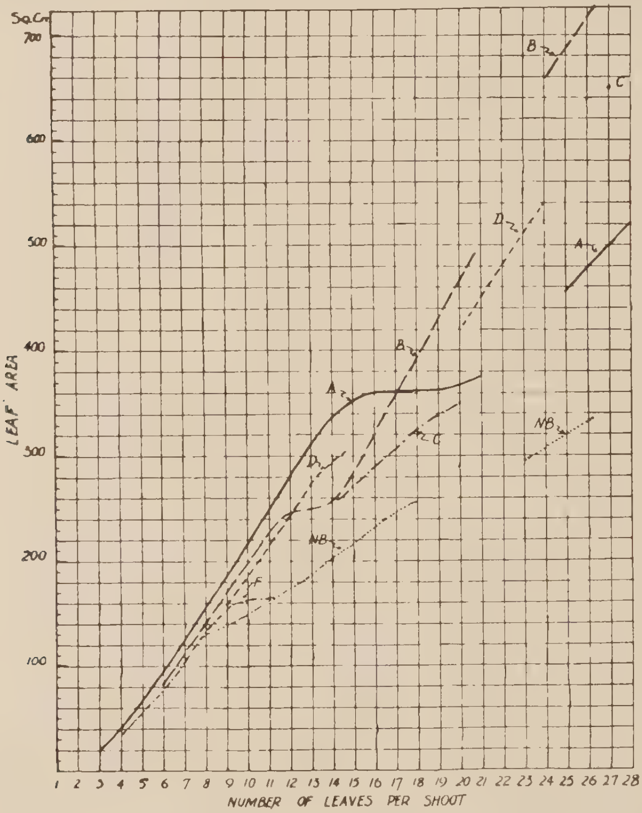

FIG. 5.

Relation of the number of leaves to the leaf area of shoots.

by each leaf number class through the entire range of classes. The main effect was carried to the highest leaf number class (*15*) in A, to a lower class (*12*) in B and C, still lower (*9*) in the fruiting tree and lowest (*7*) in the off-year tree.

From these relationships it can be seen that the frequency distributions of leaf area would be less J-shaped than those of leaf number.

Relation of Number of Leaves to Length of Shoots.

An average shoot length of each leaf number class was calculated, and is given in Fig. 6. These data show similar effects from fruit removal on length as on area per leaf number, except that there was little effect on length in the 3 to 7 leaf classes. Beyond 7 leaves the effect of fruit removal was quite apparent. In that part there were small increments of length with increases in leaf number, indicating that conditions for growth were generally poor, probably because of great competition for nutriment between growing shoots and leaves ; but when

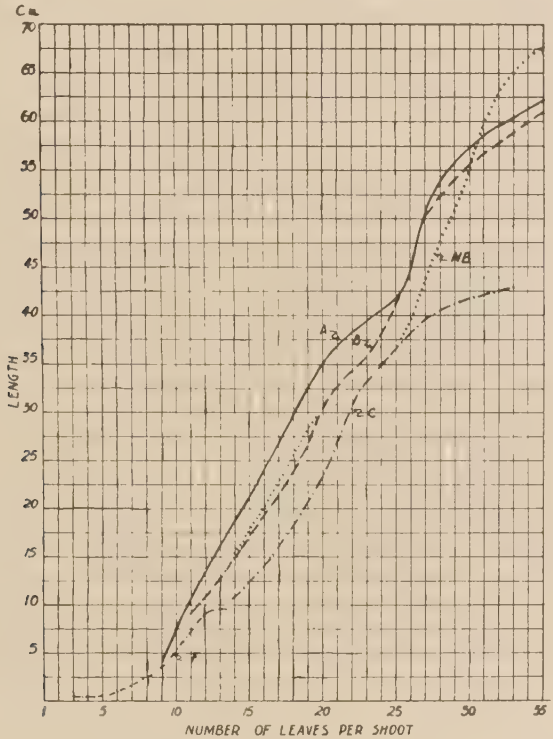

FIG. 6.

Relation of the number of leaves to the length of shoots.

this was removed by the cessation of spur growth, other shoots were able to make large increments of length for increases in leaf number.

The fluctuation in the relationship at and after 20 leaves may have been the result of cyclic growth which occurred in long shoots.

The general relationship of leaf number to length of shoots at once indicates that length frequency distributions will be more J-shaped than leaf number. The 3- to 6-leaved spurs comprised the bulk of the leaf number distributions, and since these classes fell within the one centimetre length class, it is apparent that the frequency distributions of shoot lengths will be distinctly J-shaped.

PART III.

Chemical Composition.

A chemical basis for alternate cropping was first investigated by Hooker (24, 25), who concluded that, in apple trees, carbohydrates were deficient in the on-year and nitrogen in the off-year, and that these deficiencies robbed the spurs of their individual blossoming responses and caused them to blossom or not to blossom as a whole. In on- and off-year Sugar Prune trees, Davis (12) found differences in composition similar to those in the apple, except that the content of nitrogen was the reverse of what had been shown in apple material. In the off-year, when blossom buds were formed, the percentage of reducing substances was lower, while the total nitrogen and starch (the largest variable) were higher than in the on-year. In this material Compton (10) found a higher phosphorus content and Davis (13) a higher percentage of potash and ash in the off- than in the on-year. Magnesium and calcium were not so clearly affected or consistent in the different fractions examined. However, Potter and Phillips (42) considered that bearing and non-bearing spurs were not directly comparable and analysed only non-bearing spurs. They found that blossom bud formation was constantly associated with insoluble nitrogen ; that it showed as close a relationship with the carbohydrate/nitrogen ratio as with insoluble nitrogen ; that other factors, such as the accumulation of soluble carbohydrates, have a considerable bearing ; that the accumulation of starch before July was not an indication of blossom bud formation ; that blossom bud formation was particularly associated with high fresh weight and absolute amounts of soluble and insoluble solids. More recently, evidence on this question has been provided from length of day experiments. Platenius (40) concluded that " the formation of reproductive organs is not determined by nutritional factors that involve the whole plant ", but probably by " the localized accumulation of some chemical compounds in the meristematic cells ".

With regard to the effect of thinning on composition Aldrich (1) showed that apple trees which had been thinned so as to produce blossom buds accumulated carbohydrates within three weeks after thinning. Waring (53) found very inconsistent effects on the composition of the Lombard plum from thinning at the usual time.

Potter *et al.* (41) examined the effect on the composition of Oldenburg apple trees deblossomed to the extent of 100 per cent. and 50 per cent. as compared with that of a bearing tree. The completely deblossomed tree showed distinctly higher accumulation of starch, lower nitrogen, higher phosphorus and ash than the bearing tree. Due to fluctuations in reducing sugars and sucrose, no constant differences were found in these constituents, although the data showed lower

reducing sugars in the deblossomed tree late in the season. Davis (12) found that a completely deblossomed Sugar Prune tree gave values for reducing sugars intermediate between those of a bearing and a non-bearing tree ; it rather resembled a bearing tree in starch content, a non-bearing one in nitrogen content of the bark, but a bearing one in nitrogen content of the wood and spurs.

MATERIAL AND METHODS.

Material. Spur and lateral shoot material was collected for analysis during May, June and July, thus amply covering the period of blossom bud formation. Sufficient spurs were also collected between blossoming time and the beginning of May to enable moisture determinations to be made. Usually, six one-year-old laterals were collected, stripped of their current season's terminal and axillary growth, divided into wood and bark and their dry weight determined. The axillary spurs provided sufficient material for moisture determinations. As these operations took several hours, the laterals were placed in cold store at 32° F. after collection and were brought out in rotation for preparation.

Methods of analysis. Drying : The samples were cut up finely by pruning shears and dried either in a vacuum oven at 55°-60° C. or at 55° C. in a large evaporator with an air circulation system. Dry weight was obtained after drying for 24 hours. The samples were ground in a Wiley mill to pass a 90-mesh-to-the-inch sieve.

Extraction and clarification were carried out by official methods (4).

Free reducing substances were determined, usually immediately after clarification, in a 1/5th aliquot part, using the Quisumbing and Thomas method of reduction and the sodium thiosulphate method of determining the copper. The free reducing substances were calculated as invert sugar from Quisumbing and Thomas's Sugar Tables.

Sucrose was considered as the difference between free reducing sugars and total sugars.

Total sugars were determined on an inverted 1/5th aliquot part of the above cleared solution, after inversion overnight with 10 millilitres of hydrochloric acid (S.G. 1·109).

Starch. The dry residue used for starch determination was boiled for exactly 3 minutes to gelatinize the starch and, after cooling, was kept at 37° C. for 12 hours with 5 millilitres of 0·1 per cent. diastase solution (20, 21). After this period, the solution was filtered under suction, the filtrate washed several times and transferred to a 250 millilitre flask, neutralized and made up to volume. The reducing power was determined on a 1/5th aliquot part by the same procedure

as that used for free reducing substances. Starch was expressed as glucose, from Quisumbing and Thomas's Sugar Tables, multiplied by the factor 0·95.

Total ash, soluble and total nitrogen, phosphorus and potash analyses were carried out by courtesy of the Michigan Agricultural Experiment Station, using official methods.

Expression of results. The data were calculated on a dry and a fresh weight basis. Following the usual practice, they are presented here on a dry weight basis. The differences between the fruiting tree and the defruited trees appear less on the dry than on the fresh weight basis, as the dry weight basis eliminates the effect of the significant differences in moisture content between these trees after April 14th.

Presentation of Data.

Moisture.

Certain times of fruit removal caused distinct changes in the moisture content, especially that of the spurs. The data appear in Fig. 7. In this material, blossom removal (A) caused a considerable but temporary reduction in moisture content which returned again to that of a normal fruiting tree within 20 days of full bloom. Fruit removal at 16 days (B) also caused a marked, temporary reduction in moisture, but less in degree and duration than in A. Fruit removal at 30 days (C) and at 47 days (D) did not affect the moisture content immediately after removal.

After the temporary reduction in moisture content of A and B, these trees and also C and F had a similar moisture content to the fruiting tree on April 14th.

The fruiting tree then gained in moisture content over the defruited trees, and showed a higher moisture content for the rest of the season.

The defruited trees A, B and C had similar moisture percentages until late June and July, when they showed more scattered values. Fruit removal at 47 days (D) gave values intermediate between those of the fruiting tree and the defruited trees.

These results differ from the fewer data of Davis (12) who found that the moisture content increased up to the last day of April or the first day of May in all fractions (bark, wood and spurs) of both bearing and non-bearing trees. In the fractions from the bearing trees, the amounts of moisture remained reasonably constant for the remainder of the season, in those from the non-bearing trees they began to fall about May 1st.

The clear effect of fruit removal on the moisture content of the spurs was not shown in the wood and bark of laterals and only during May in the axillary spurs from laterals. The effect, therefore, is one that is localized in the spurs, thereby differing from that on other constituents to be discussed.

Reducing Substances.

Fruit removal produced a distinct change in the content of reducing substances. The data appear in Fig. 8. The content of reducing substances in the trees from which fruit was removed was similar to or higher than that in the fruiting tree until May 20th, when it became less and remained so for the rest of the season. All fractions showed a similar change. The content of reducing substances was similar in all the defruited trees, irrespective of the time at which

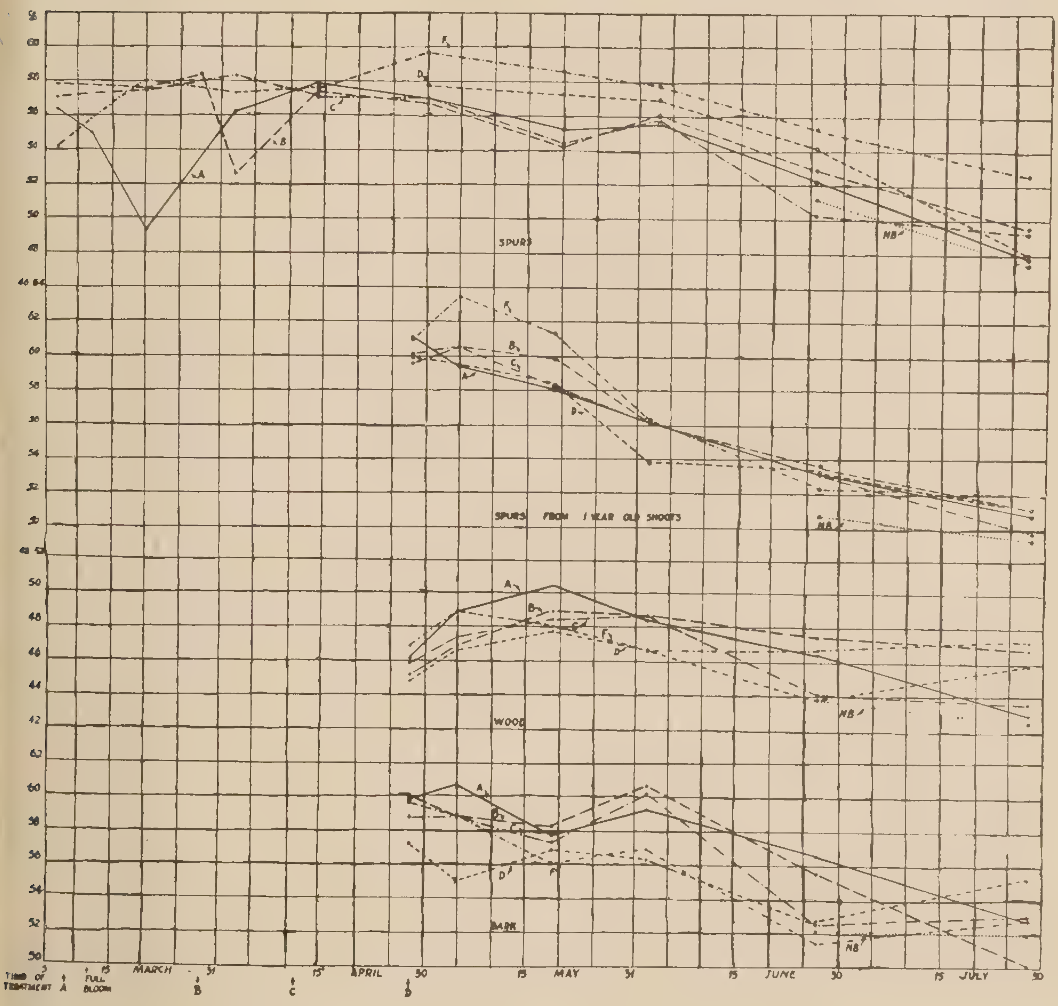

FIG. 7.

Moisture content, as percentages of fresh weight of spurs, axillary spurs from one-year old laterals, and the wood and bark of laterals.

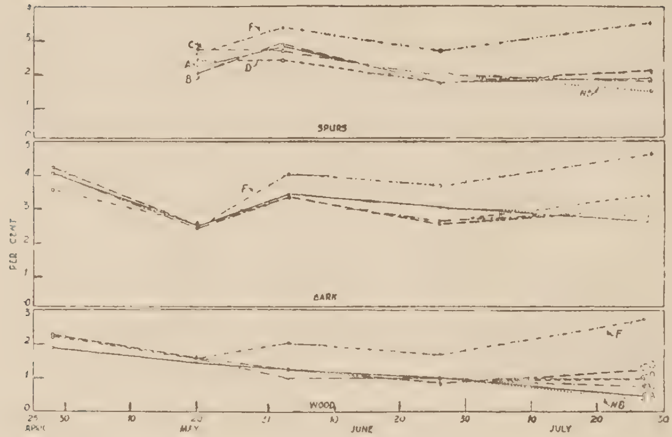

FIG. 8.

Reducing substances content, as percentages of dry weight, in spurs and in the wood and bark of laterals.

the fruit had been removed. and the content of the defruited trees was similar to that of an off-year tree in June and July.

It appears, then, that the seasonal changes in reducing substances of the defruited trees resemble those of an off-year tree as described by Davis (12). Davis found, however, that debudded material (i.e. corresponding with treatment A of the present study) had a content of reducing substances intermediate between that of an off- and an on-year tree.

TABLE XII.

Sucrose as Percentage of Dry Weight.

Material.	Treatment.	April 28th.	May 20th.	June 3rd.	June 26th.	July 28th.
Spurs	A	—	0·1	1·4	1·3	1·8
	B	—	0·1	1·2	1·4	1·2
	C	—	0·1	0·1	0·7	1·2
	D	—	0·1	0·2	1·0	2·1
	F	—	0·1	0·1	0·5	1·0
	NB	—	—	—	0·8	1·4
Bark	A	2·1	2·3	2·0	1·0	2·3
	B	1·8	2·1	1·6	2·1	2·1
	C	2·1	2·5	2·5	1·5	2·0
	D	2·0	2·2	1·8	1·0	2·0
	F	2·1	2·2	1·5	1·0	1·5
	NB	—	—	—	1·2	1·3
Wood	A	0·4	0·4	0·4	0·4	0·1
	B	0·3	0·4	0·4	0·5	0·2
	C	0·2	0·4	0·4	0·3	0·1
	D	0·2	0·4	0·4	0·4	0·1
	F	0·3	0·3	0·2	0·2	0·1
	NB	—	—	—	0·3	0·4

Sucrose.

The trees from which fruit was removed tended to have an increased sucrose content after May 20th, whereas the fruiting tree showed a low level of sucrose content. The data are given in Table XII.

Starch.

All the trees from which fruit was removed showed a higher starch content than the fruiting tree. The data appear in Fig. 9. In the fruiting tree, starch was low until June 3rd, when it showed some accumulation. All the defruited trees, however, despite differences of time of fruit removal, showed a comparatively high starch content which increased during the season and in June and July was only somewhat lower than that of the off-year tree.

Nitrogen.

Total Nitrogen. During the season the defruited trees showed a level to slightly increasing content of total nitrogen, whereas the fruiting tree, although it started with the highest content, steadily declined in total nitrogen. The defruited trees had a distinctly higher percentage of this constituent than the fruiting tree after May 20th. All trees from which fruit was removed had rather similar amounts of total nitrogen, which, in the June and July samples, were not quite as high as that of the off-year tree. The data confirm Davis's finding that the non-bearing spurs of the Sugar Prune are lower in nitrogen than the bearing spurs, a condition which is contrary to that in apple spurs as established by Kraybill and associates (27, 28) and Hooker (24).

The separation of total nitrogen into soluble and insoluble fractions is of particular interest because of the different seasonal trends and the effect of fruit removal on them. The soluble fraction is more variable in content. The data appear in Fig. 10.

Soluble Nitrogen. The defruited trees differed from the fruiting tree in seasonal trend ; at the end of April they started with a low content of soluble nitrogen and, except C, showed an increasing content till the end of July. The fruiting tree started with the highest content in April, showed a steeply declining content in May and June and ended on July 26th with the lowest content of soluble nitrogen. The defruited trees were lower than the fruiting tree in early May, similar to it in late May and early June and higher in late June and July. At the latter times, the defruited trees gave lower values than the off-year tree.

Insoluble Nitrogen. At the end of April, the fruiting and the defruited trees had a content of insoluble nitrogen rather similar to that of A, B and C, at a higher

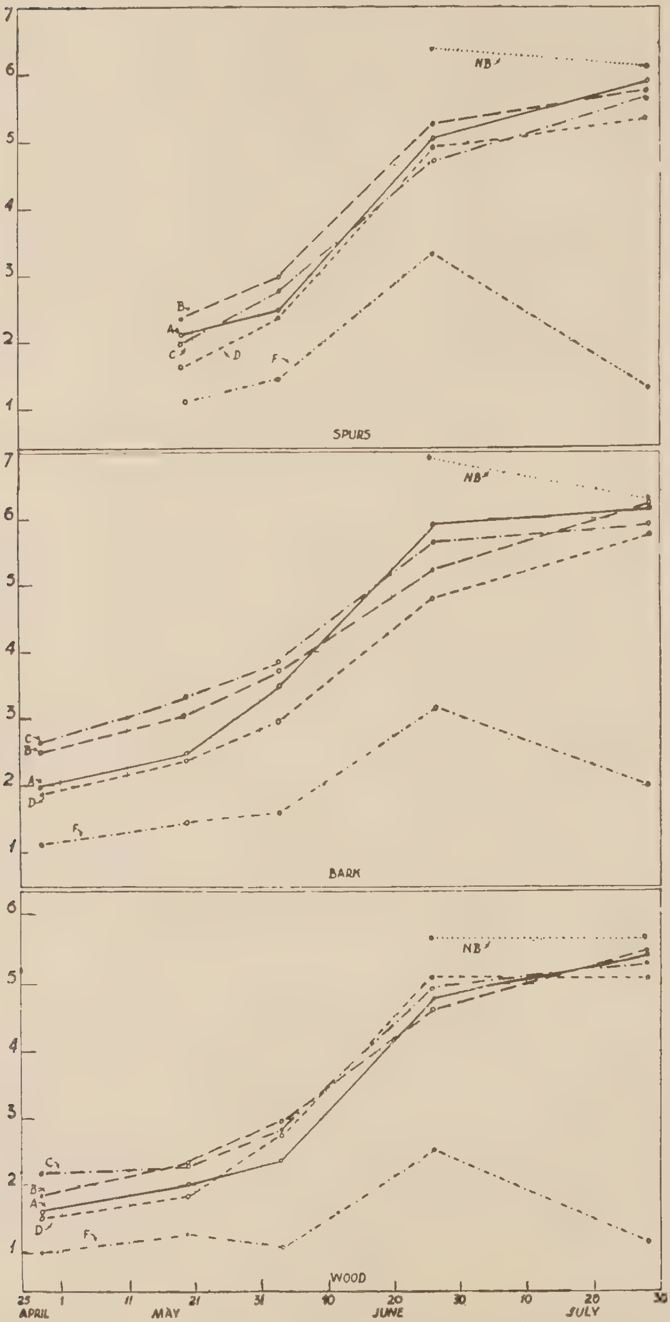

FIG. 9.
Starch content, as percentages of dry weight, in spurs and the bark and wood of laterals.

level than that of D and F. Thereafter, all the defruited trees showed a comparatively constant content of insoluble nitrogen, but the fruiting tree steadily declined in this constituent. Tree D was similar to a fruiting tree on April 28th, but by May 20th was similar to other defruited trees.

Total Ash.

Contrary to expectation, the fruiting tree did not differ from the other trees in ash content until late July. At this time F and D showed a lower ash content than the defruited trees and the off-year tree. Tree C was outstanding for high ash content in June and July. The data are given in Fig. 10.

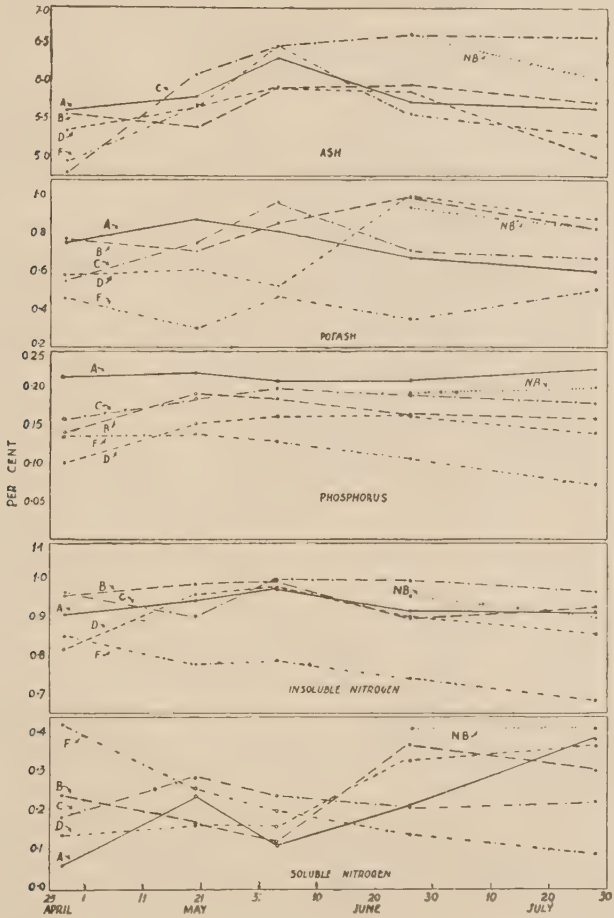

FIG. 10.

Ash, potash, phosphorus and insoluble and soluble nitrogen content, as percentages of dry weight, in the bark of laterals.

Potash.

Fruit removal had a distinct effect on the potash content. The data, as percentages of K_2O, appear in Fig. 10. At the end of April trees A and B (early times of fruit removal) already showed a higher content of potash than the fruiting tree, and trees C and D (fruit removal at 30 and 46 days, respectively.) had an intermediate amount of potash.

Within a month tree C had a similar content of potash to that of the other defruited trees, and after two months D had reached a similar level. With these exceptions the defruited trees maintained a distinctly higher level of potash than the fruiting tree from the end of April to the end of July. At this time the fruiting tree increased in potash content, probably due to migration from the leaves, such as has been shown by Lilleland and Brown (32) to take place from the leaves of the d'Agen prune in California after July.

Phosphorus.

During the period of analysis, all the trees from which the fruit was removed showed a level or slightly increasing content of phosphorus. The fruiting tree, however, showed a slight decrease during the season with the result that it had a lower content of phosphorus after May 20th. Among the defruited trees, blossom removal (A) gave the highest value, and fruit removal at 45 days (D) gave the lowest. In tree A the seasonal trend was level ; trees B and C started with lower amounts but increased to higher levels by May 20th ; tree D started with the lowest content of phosphorus and increased to a level inferior only to that of other defruited trees by June 3rd. At the time of the June and July sampling, the phosphorus content of the defruited trees was similar to that of the off-year tree. The data expressed as percentages of P_2O_5 appear in Fig. 10.

Discussion.

Influence of fruit removal on composition. Fruit removal altered the composition towards that of an off-year tree, as indicated by the comparable off-year tree samples of late June and July. Trees from which fruit was removed thus showed a similar kind of difference from the fruiting tree to that which has been reported between on-and off-year trees in reducing substances, starch, nitrogen, potash (12, 13) and phosphorus (10). In addition, the early times of fruit removal, A and B, also caused early, marked and temporary reductions in moisture content, although C did not ; all times of fruit removal altered the moisture content of a fruiting tree after April 14th.

Fruit removal at the latest time (D) did not change the composition as soon as did the earlier times of fruit removal. Carrying fruit for a period of 47 days prevented tree D from reaching a high content of potash and phosphorus till

108 days after full bloom, and of nitrogen, till 70 days after full bloom. It thus gave intermediate values for potash, phosphorus and insoluble nitrogen in May.

Relation of composition to blossom bud formation. Apart from these intermediate values in D the composition of the four defruited trees, particularly during June and July, does not indicate any constituent which was critically associated with the blossom bud formation of A, B and C, or the absence of blossom bud formation in D. On Raglan's (45) findings blossom primordia would have been appearing from the middle to the end of June. The similarity in composition between trees A, B, C and D at the time of blossom bud formation contrasts very sharply with the large differences in growth that appeared in them from the critical time onwards.

These results do not support the view that the general composition of the spurs, or the tissue adjacent to them, such as the bark and wood of one-year old laterals, which bear many spurs, is the determining factor for blossom bud formation.

PART IV.

Growth of the Fruit.

In on-year Sugar Prune trees which were defruited after the critical time, or which carried their fruit to maturity, the buds failed to develop into blossom buds, the reason for this being the curtailment of growth at about the critical time. The influence on growth and also on composition of the fruiting processes—flowering, rate of fruit growth, and the shedding process—will be described in this section.

Method.

Flowering and setting. The original number of blossoms was recorded and the set of fruit was counted periodically on five representative branches selected at random around trees B, C and F. The fruit that would drop at each time of record was shaken from the trees, and omission of this from the records of set fruit facilitated records of the setting process. The number of leaf buds was also recorded so that setting could be expressed on the basis of leaf-bearing spurs.

Development of the fruit. Samples of fruit varying from 100 during the first month, 20 during the second and 15 thereafter, were taken from the fruiting tree (F) to determine the seasonal increases in fresh and dry weights, and in volume by displacement of water.

The samples were cut into small pieces and dried in a forced draught oven at 55-60° C. The pericarp and the kernel or seed were recorded separately after

April 16th, 35 days after full bloom. Determinations of fresh and dry weight and of volume were made on samples of the dropped fruit.

Presentation of Data.

Flowering.

The excessive blossom bud formation in the previous summer completely inhibited leaf and shoot growth in 15 to 24 per cent. of the buds in the on-year of 1936. This is shown in Table XIII as the proportion of blossoming shoots without leaves to those with leaves and to leafy or non-bearing shoots.

A similar but accentuated condition was communicated to the author by Dr. Davis in 1938, the next on-year. The results appear in Table XIII.

Of the trees examined in 1938, tree 3/5 was the fruiting tree of the present investigations ; tree 7/1 was one of the smaller and more precocious trees in the Sugar Prune block, and the group marked rows 15 to 16 was a composite of two trees from each row. Tree 7/1 and group 15/16 had not been used in the

Table XIII.

The Percentages of Leaf- and Flower-producing Shoots.

	On representative limbs, 1936.			On representative limbs, 1938.			On spur clusters only, 1938.		
	B.	C.	F.	tree 3/5(F)	tree 7/1	rows 15/16	tree 3/5(F)	tree 7/1	rows 15/16
Blossoming shoots—									
(*a*) Without leaves ..	23·7	31·0	14·8	25·4	38·5	27·5	28·0	42·0	29·2
(*b*) With leaves	49·8	63·0	61·1	66·8	49·7	60·7	69·5	56·8	69·8
Leaf shoots, without blossoms	26·5	16·0	24·1	7·9	14·8	11·8	2·5	1·3	0·9
Leaf shoots, with and without blossoms	76·3	79·0	85·2	74·7	64·5	72·5	72·0	58·1	70·7
Number of shoots examined	533	481	643	694	1,020	752	575	737	564

present investigation. The trees sampled had not been subject to any fruit thinning treatment and were, therefore, deeply entrenched in the alternating habit.

The differences between the 1938 and 1936 data would indicate that these prune trees were increasing in fruitfulness in succeeding on-years. There were relatively fewer leafy shoots and more leafless ones bearing spurs in 1938 than in 1936.

Off-year trees produced some 30 per cent. of the shoots (practically all being small spurs) from dormant buds in the old spur clusters, and thus maintained the number of spurs from year to year. Yet the 15 to 24 per cent. bearing spurs that were without leaves depended on the leafy spurs and thus the set per spur described later is expressed on the basis of leafy shoots.

SEASONAL DEVELOPMENT OF THE FRUIT AND SEED.

Fruit.

The growth of the Sugar Prune showed the three phases characteristic for stone fruit (11, 16, 50, 51, 29, 30). It is preferable to regard this development as a double growth curve in which the parts were as follows :

				Days in each period.	Days of growth.
Phase I.	1st growth curve part	*a.*	March 12th-April 2nd	21	21
	,, ,, ,, ,,	*b.*	April 2nd-May 7th	35	56
Phase II.	,, ,, ,, ,,	*c.*	May 7th-May 18th	11	67
	2nd ,, ,, ,,	*a.*	May 18th-June 1st	14	81
Phase III.	,, ,, ,, ,,	*b.*	June 1st-June 26th	25	106
	,, ,, ,, ,,	*c.*	June 26th-July 25th	29	135

The fresh and dry weight increases of the entire fruit and of the seed are given in Fig. 11. The seasonal increases in volume, fresh and dry weight of the fruit agreed closely with one another.

The hardening of the endocarp first became evident during Phase I, but took place rapidly early in Phase II. On April 24th about 50 per cent. of the setting fruit showed a slight hardening at the distal end of the endocarp. By April 30th, the stones or pits were rapidly hardening along the ventral suture ; by May 7th, they had hardened throughout but were still capable of being cut with a knife. By May 18th, they were hard enough to turn the edge of the pruning shears used to cut the fruit. The hardening process thus extended from 42 days to 67 days after full bloom, i.e. the last 25 days of the first growth curve.

The percentage dry weight of the fruit was affected by the cyclic growth. It was high in parts *a* and *c*, and low in part *b* of each growth curve. As the prune is allowed to hang until it drops, it differs from the dessert stone fruits in part *c* of the second growth curve where it reached a very high percentage dry weight. At this time its fresh weight remained constant, but its dry weight increased considerably.

Seed.

The development of the seed took place in several distinct stages. First in Phase I there was a growth of the integuments and the nucellus. Then, coinciding with rapid pit hardening in Phase II, followed a development of the endosperm, which was visible to the naked eye, about the size of a pin's head, on April 28th. The endosperm had grown to the extent of occupying half the nucellus by May 18th. The embryo also appeared at this time, the cotyledons occupying half the endosperm, and by June 3rd it was fully grown and filled the seed coats. In Phase III the cotyledons increased in firmness and dry matter.

The foregoing development of the seed relative to the fruit agrees with the findings of Lilleland (30) for other plum varieties and with Tukey (50, 51) for peaches.

These stages of development are reflected in the fresh and dry weights and the percentage dry weight of the seed, the records of which are given in Fig. 11. The notable increases in fresh weight and the slight increases in dry weight of the nucellar stage were associated with part *b* of the first curve of fruit growth. Slight but consistent decreases in percentage dry weight occurred at this time. The fresh weight fell sharply and the dry weight slightly between April 30th and

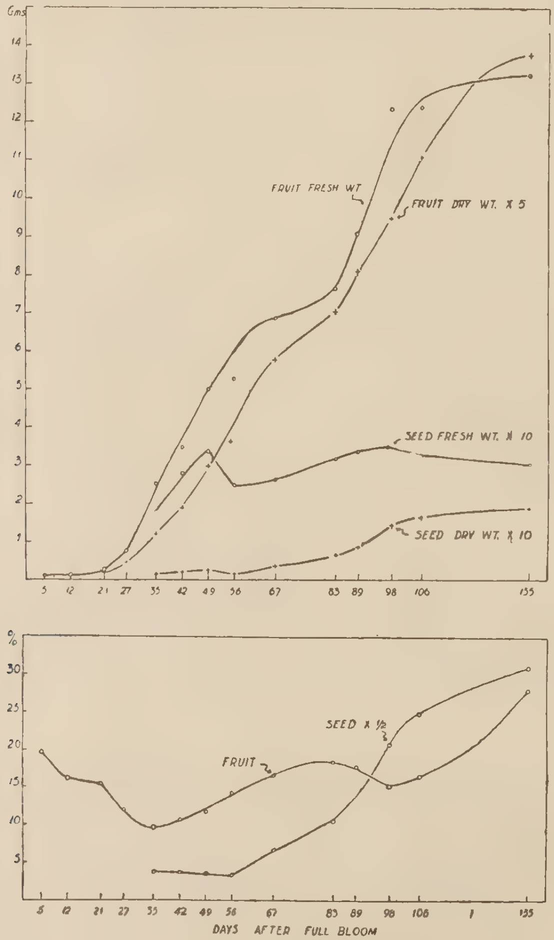

FIG. 11.

Fresh and dry weight increases of the fruit and the seed (above) and the seasonal changes in percentage dry weight (below).

May 7th, coincident with the earliest macroscopic appearance of the endosperm. The subsequent increases in fresh and dry weights and in percentage dry weight were associated with part *c* of the first curve and with the second curve. Fresh weight increased only in parts *a* and *b* of the second curve, but dry weights and percentage dry weight increased till harvest.

The changes in percentage dry weight were extremely large, namely from 6·9 on May 7th to 62·0 on July 25th.

Fruit Shedding.

In the Sugar Prune the number of flowers, the extent of the three fruit drops and the final setting on the sample limbs of the fruiting tree (F) are given in Table XIV. The decline in the number of fruits per spur (leaf bearing) is shown

Table XIV.

Summary of Fruit Shedding from the Fruiting Tree (F).

	No. of fruit at the start and end of each drop.	% Fruit falling in each drop.
Number of flowers	1,682	
1st drop—ended April 2nd	1,682 -1,242	26·15
2nd drop—ended April 24th	1,242 - 563	40·35
3rd drop—ended June 18th	563 - 356	12·3
Number of fruits set	356	21·2

in Fig. 12 (upper graph). The first shedding was smaller than the second, and the third, or June drop, was comparatively small. The remaining set of 21·2 per cent. was heavy and resulted in small fruits.

Shortly before ripening a slight shedding of maturing fruit took place, which amounted to 2·7 per cent. of the final set of fruit. The characteristics of the sheddings agreed with the findings of Dorsey (14).

The Initiation of Fruit Shedding.

The data reported here provide a means for discovering the time of initiation of fruit dropping and therefore of ascribing causal factors. The period of initiation was found by tracing back the dry weight of the drop fruit, to the growth curve of the setting fruit. This is shown in Fig. 12.

The second drop fruits recorded on April 8th, 16th and 24th were similar in weight and traced back to April 3rd.

The remaining fruits at that time showed differences in size, the smaller ones having turned yellow at the stalk end, identifying them as the June drop. This fruit was the start of the next drop, 3*a*, which was sampled again on

April 30th and May 7th. This drop fruit showed no pit hardening. It traced back to April 12th, when the set fruit was showing the increased rate of growth in its first cycle of growth and showed traces of pit hardening. Additional drop fruits were noted and their dry weight recorded on May 7th. Although slightly heavier, this fruit was a later phase of the same drop. It traced back to April 15th instead of the 12th, and thus came within the same phase of fruit growth.

Later fruits that dropped (called 3*b*) were more advanced in development than that of 3*a*; on June 3rd, they had partly developed pits and on June 18th

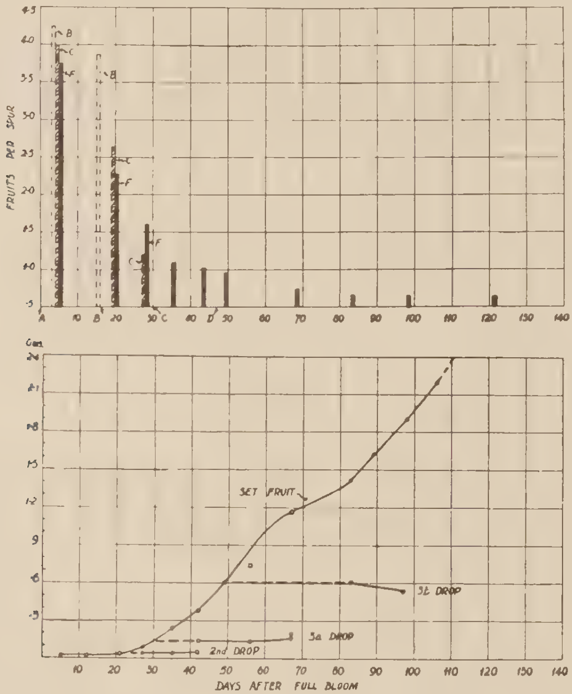

FIG. 12.

Number of fruit per spur (above) and the dry weights of the drop fruit traced back to the growth curve of the fruit (below).

had imperfectly hardened or very thin entire pits. Embryos had aborted when they were 2 to 3 millimetres long or when their cotyledons had made slight growth. Both samples traced back to April 30th, 48 days after full bloom, which immediately followed the first record of endosperm development and pit hardening in the set fruit.

The dry weight of the set fruit on May 7th is lower than that shown in the interpolated curve. This is probably due to a mixture of set and "about-to-drop" fruits having been sampled, which, as both were green although of

different sizes, were not distinguished from each other on this date. This accords with deductions that the 3*b* drop was in process of initiation at this time.

In brief, it is considered that the drops were initiated as follows :—

2nd drop on April 3rd, 22 days after full bloom ;

3*a* drop on April 12th, 31 days after full bloom ;

3*b* drop on April 30th, 48 days after full bloom.

That is, these drops, except 3*b*, were initiated by the critical time, notwithstanding the lengthy period of the dropping process, which, since the 3*b* drop had finished by June 18th, lasted 98 days. However, the fruit of the 3*a* drop had not commenced to drop by the critical time.

The possible cause of fruit shedding may be examined, now that the time at which each drop is initiated has been arrived at.

The second drop is initiated at the inception of part *b* of the first growth curve, and indicates a lack of the growth stimulant that activates the setting fruit into the rapid increases in size of the first growth curve. The 3*a* drop is initiated in part *b* of the first growth curve and may occur because of the competition for nutrients during this active growth. The cause, however, must be of a particular kind, as the three separate records of this drop trace back to the one time, April 12th. The 3*b* drop is initiated with early endosperm and embryo development. The failure of this tissue to grow from cytological and genetic causes, removes this stimulation to the growth of the fruit which thus fails to compete and survive. Moreover, competition would be stronger at this time because of the inception of pit hardening. All the drops were initiated as the percentage moisture, and therefore the physiological activity of the fruit, was increasing rapidly.

DISCUSSION.

The Relation of Fruiting Processes to the Critical Time.

By the critical time of 35 days after full bloom, the fruit had entered its period of rapid growth in the first growth cycle, and its percentage of moisture was the highest in the seasonal curve ; the seed was in the nucellar stage and the early third drop had already been initiated, but had not appeared as sheddings. The growth rate of the fruit at this time offered a substantial check on vegetative growth and one that had been increasing since the fruit entered its rapid period of growth, 20 days after full bloom.

It is a sufficiently additional drain on the nutrition (already at minimum levels in the first month) that by 35 days, fruit growth limits rather abruptly that of the great majority of the shoots and leaves, and, it is considered, on the basis of the growth regulating substance hypothesis presented in Part II,

before these shoots and leaves can bring about the necessary change in development within the buds which will culminate in blossom bud formation.

The check that the rapid growth of the fruit imposed is illustrated in the frequency distributions and the seasonal growth of leaves. In A, B, C, D and F the frequency distributions were altered with the progressively longer periods of fruiting in the following manner :—

1. Heightening of the modal class.
2. Reduction of the frequencies in the classes immediately following the mode.
3. Reduction of the longer shoots (laterals) in number (that is, percentage of the sample) and in length (that is, range of classes).

As the shoots longer than the mode grew later than the shorter ones they were inhibited by the longer periods of fruiting of C, D and F. This inhibition added to the frequencies and caused a heightening of the modal class.

The seasonal development of the leaf areas of trees A, B, C and F, which were similar for 26 days after full bloom, showed differences by 35 days because of the differential expansion of distal leaves which accounted for the main increases in area. The differences in seasonal expansion of leaf area were established only after the fruit started to grow rapidly, although A had been deblossomed, and B defruited 19 days earlier and C 5 days earlier than 35 days after full bloom.

At first sight, the death and abscission of the terminal point of the spurs, which was observed from April 14th to 16th, would appear to be related to part *b* of the first growth curve, but it also appeared in tree (A) and in the off-year tree (NB).

That an off-year tree showed a growth of leaves and shoots, essentially similar to that of a fruiting tree, indicates that fruit development is merely an additional factor that limits growth. However, when this factor was removed or reduced, especially as seen in part *a* or early in part *b* of the first curve, vegetative growth increased considerably as compared with either a fruiting or an off-year tree. These increases probably derive from the higher reserves of carbohydrates and other nutrients with which, as shown by Davis (12, 13), a bearing prune tree enters the on-year. Mack (33) also observed that if anything prevents the set in the on-year of biennial apple trees, growth is considerably more than that of the off-year tree.

A reciprocal and quantitative relationship appears to exist between the first sigmoid curve of fruit growth and the reversely sigmoid one of the mean shoot and leaf growth of the defruited trees. This will be seen by superimposing Fig. 11 upon Fig. 4. A and B fall in part *a*, C early in part *b*, D later in part *b* ; and 9 weeks, which, by interpolation, would give similar growth to F, coincides with limit of part *b* of the first curve of fruit growth.

The influence of fruit growth on composition. Fruiting caused certain clear and orderly changes in composition. It caused clear departures from the defruited trees in the content of moisture, reducing substances, sucrose and starch, nitrogen, potash and phosphorus. The departure in moisture content of the spurs began after April 14th ; in insoluble nitrogen, potash and phosphorus after April 28th ; in reducing substances and sucrose after May 20th ; and in soluble nitrogen after June 3rd. After the above-mentioned dates, the fruiting tree showed a higher content of moisture and of reducing substances and a lower content of sucrose, starch, potash, nitrogen and phosphorus.

Considerable interest attaches to the order in which these changes appeared and to the question whether they are necessarily connected with one another. Moisture was first affected, then the ash elements and finally the carbohydrates.

To deal first with the last-named, after May 20th, the bearing tree showed a combination of high reducing substances, low sucrose and low starch. If it may be assumed that reducing substances were reducing sugars, it appears that the bearing tree was unable to form the higher condensation carbohydrates, and therefore that the storage of lower carbohydrates of a fruiting tree was initiated by the failure of reducing sugars to condense to sucrose. Reducing sugars thus accumulated in bearing trees to a higher level of nutrition than in trees without fruit.

Next, it is a point for consideration whether the changes in carbohydrate metabolism derive from the effect of fruiting on the mineral constituents. The investigations of Phillips, Smith and Dearborn (39) and of previous workers cited by these authors, indicate that a disorganization of the usual carbohydrate metabolism is characteristic of the early stages of a deficiency of potash. In the prune material, insoluble nitrogen and phosphorus were affected as well as potash, although the potash being affected earlier and more strongly by fruiting has priority as a cause for the different carbohydrate metabolism of a fruiting tree.

Following the elucidation of these changes in composition of the bearing tree, a re-examination was made of the literature, and this afforded some material with which to compare the bearing tree, the chief being that of bearing and non-bearing trees. The extensive data, provided by Davis (12, 13) and by Compton (10) on alternate bearing Sugar Prunes show quite clearly a departure of the bearing trees from the non-bearing trees in reducing sugars, nitrogen, ash, potash, and phosphorus similar to that reported herein. In general, this change occurred in the bark and wood, and in spur material, on April 30th to May 15th, more often on the later date in the wood than the bark. In addition, the content of calcium and magnesium became lower in the off-year tree at about the same time. Lilleland (31) presented the content of potash and phosphorus, calcium and magnesium, as milligrams per leaf in the leaves of bearing and defruited

French Prune trees. The latter had a distinctly lower content of potash and phosphorus and a similar content of calcium and magnesium. The onset of the differences was not shown.

In the apple, the evidence for the effect of fruiting on the different constituents and the time of change is not so consistent, although this might be expected from the different nutritional levels at which trees in widely different places would commence the season. Hooker's (24) data indicate a clear influence of fruiting on the content of reducing sugars, potash, phosphorus and nitrogen, beginning early in June. Potter and Kraybill (41) also showed an influence on reducing sugars, nitrogen and phosphorus, which appeared in July. In this instance, the seasonal increases in the dry matter of the fruit being presented, the influence could be traced to the period of most rapid increase of dry matter in the fruit. Kraybill (27, 28) showed the existence of some influence on the content of moisture, nitrogen, phosphorus and ash, the differences appearing early in the season. All analyses showed a strong effect on starch content.

However, the changes that have been described as due to the influence of fruiting may not derive from one another but may stand in separate relationship to the distinct stages of growth of the fruit. This view is suggested by the fact that tree D was defruited late enough to affect the contents of moisture, potash, phosphorus and insoluble nitrogen as in a fruiting tree, but not the carbohydrate content, especially the reducing substances, which were similar to those in other defruited trees. The moisture content change (33 days after full bloom) occurred when the fruit entered part *b* (rapid growth) of the first growth curve and became high ; the change in phosphorus, potash and insoluble nitrogen contents (48 days after full bloom) took place at the latter end of this period of growth and at pit hardening ; the changes in reducing sugar and sucrose (after 70 days from full bloom) occurred at the very inception of the second growth curve.

As all the times at which fruit was removed occurred during the first growth curve and caused a general change in composition towards that of an off-year tree, it is clear that the early stages of fruit development alone did not have a permanent effect on composition. Fruit removal at 47 days (D), however, was late enough to give intermediate values in moisture, potash and phosphorus content in May and in insoluble nitrogen at the end of April. In other words, it is the continued growth of the fruit in the second growth curve that brings about changes in composition.

Additional definite information on these changes would be a valuable guide to certain horticultural practices, such as ordinary fruit thinning and manuring, although, since the effect is caused by the late growth of the fruit, it cannot be expected to affect the alternate cropping question, in which the interrelated growth and blossom bud formation are affected by the growth of the fruit early in the first cycle.

SUMMARY.

The influence of the time of fruit removal on growth and composition, and the relationship of these factors to a critical time (at 35 days after full bloom) for blossom bud formation, were examined in four alternate bearing Sugar Prune trees of which trees A, B and C were defruited before and tree D after a critical time.

In seasonal growth, differences of leaf area among treatments occurred between 26 and 35 days after full bloom and were due to the differential growth of the distal leaves of the spurs. The critical time occurred during the expansion of the distal spur leaves, after the cessation of spur growth in length and before the occurrence of the main diametral growth.

The methods of measuring growth are discussed and the type of frequency distributions of the prune shoots (all being primary) are shown to be extremely skewed or J-shaped, with a single mode which is in the spur classes. Such a distribution precludes the use of probable error.

Mean leaf and shoot growth showed a sigmoid reduction with the time after blossoming that fruit remained on the tree. This generalization indicates that fruit removal after nine weeks would not improve the growth over that of a fruiting tree, and that the critical period at 35 days after full bloom falls in part II of the curve, when the responses of growth to fruit removal are becoming small. The significance of the growth responses for blossom bud formation is considered (on the basis of a growth regulating substance) to be due to the comparative amount of leaf growth that took place at the critical time. Expressed on a leaf basis, the data also indicate reasons why the shoot leaf number distributions were more J-shaped than those of leaf area, and shoot length more J-shaped than leaf number.

Fruit removal at the four different times caused the composition (moisture, reducing substances, sucrose, starch, nitrogen, phosphorus, ash and potash content), closely to approximate that of an off-year tree in May, June and July. Tree D, however, showed intermediate values in May for insoluble nitrogen, potash and phosphorus content. Apart from these differences, no constituent was found to be critically associated with the blossom bud initiation of A, B and C, or with the absence of blossom bud formation of D.

In seasonal development the Sugar Prune showed a double growth curve. The changes in the percentage of dry weight of the fruit, the growth of the seed and hardening of the pit are shown relative to the growth of the fruit. By using the dry weights of the natural sheddings the time of initiation of the sheddings was allocated to definite parts of the first growth curve of the fruit. Flowering was found to inhibit completely the vegetative growth of 15 to 24 per cent. of the shoots of on-year trees.

At the critical time for blossom bud formation the fruit was in the rapid period of growth in the first cycle, the moisture content was the highest for the season, the seed was in the nucellar stage and the first, second and early third drops had been initiated. The rapid rate of growth of an excessive crop at this time is considered to impose an abrupt check on spur leaf growth which prevents a change in bud development that would culminate in blossom bud formation. This check is illustrated in the frequency distributions of leaf and shoot growth as well as in the reciprocal quantitative relation of mean leaf and shoot growth to the growth curve of the fruit.

Fruiting caused certain clear and orderly changes from the defruited trees in contents of moisture, reducing substances, sucrose and starch, nitrogen, potash and phosphorus. The cause for these changes is referred to the growth curves of the fruit. It is shown that the earlier stages of fruit growth alone, i.e. up to the critical time, did not influence the composition of the tree later in the season, although when fruit was carried for 47 days (D) an effect on composition was noticeable for a period of 30 to 50 days after that time of fruit removal.

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THE BRITISH BROWN AND GREEN LEAF WEEVILS ASSOCIATED WITH CULTIVATED FRUIT TREES AND BUSHES

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Most British leaf weevils infesting top and soft fruits are so much alike in the field that the various species have been very much confused in the past ; it seems desirable, therefore, to sort them out, and to discuss each species in some detail, in the hope that they may be identified and recorded more accurately in future.

As an example, *Phyllobius argentatus* L., the common green leaf weevil of orchards in the chief fruit growing districts of Kent, is not referred to at all in the literature, while another species, *Phyllobius maculicornis* Gm., frequently associated with the oak and hazel, and not commonly found on fruit trees, is regarded as the prevalent one on them, even in contemporary literature.

One species of *Nemoicus* (=*Phyllobius*) and four species of *Phyllobius* occur on top and soft fruits, and it is proposed to refer to each in the order of its importance.

(*a*) Brown Leaf Weevil (*Nemoicus oblongus* L.). This weevil, which cannot be confused with any other fruit-infesting species because of its brown elytra, is the most abundant species of our orchards. The adult weevils emerge from the soil in the spring about the time when Bramley's Seedling apple is coming into bloom, and they start at once to feed on its petals and tender foliage. This species attacks many kinds of plants, but it is more partial to apple, pear, plum, cherry, nut and walnut than others; in some seasons the trees suffer considerably for a short period. It is also very harmful to apple, pear and plum stocks in the nursery, while young nursery trees are frequently partially defoliated.

It is fortunate for the fruitgrower, but nevertheless a curious fact, that the leaf weevils feed on the foliage of cultivated fruits for a short period only (the usual time being about two or three weeks) before they migrate elsewhere, their sudden disappearance being as marked as their arrival in the orchard a few weeks earlier. This sudden disappearance of the weevils is difficult to explain. It may be that they prefer to feed on tender foliage only, and they find an ample supply on the oaks and hazels in the neighbouring woods and hedgerows. It should be noted that the oak comes into leaf later in the season than most of our fruit trees, and the tender foliage of the former may be more suitable to the weevils. It is at least a fact that those species of weevils which infest fruit

plantations may be found feeding on the foliage of oak and other trees and shrubs for several weeks after they have left the foliage of fruit trees.

As indicated by the generic name, all the British fruit tree loving species of *Phyllobius* are leaf-eating, and none of them feeds upon the fruits.

Very little information is available regarding the habits of the immature stages of these weevils, but recent observations indicate that the larvae of some species live in the soil, where they feed on the roots of couch grass (*Agropyrum repens* Beauv.).

Fryer (1919) records the larvae of *Phyllobius urticae* De G. and *P. oblongus* L. as attacking the roots of strawberry, causing severe damage on about thirty acres of plants. This appears to be one of the very few British records of *Phyllobius* larvae causing damage to plants of economic importance. The larvae of *P. calcaratus* F. have been recorded as a minor pest of strawberry in Germany.

The species associated with cultivated fruits occur equally commonly in England, Wales, Scotland and Ireland, and can therefore be described as being abundant throughout the British Isles.

Donisthorpe (1935) records an aberration of *P. oblongus* L. in Britain which, he states, may be distinguished from the type form by the fact that the head, thorax, elytra and the underside are quite black. This aberration is called *P. oblongus* L. ab. *floricola* Herbst. The writer is quite familiar with this so-called aberration (which occurs very commonly each season in June) but is of the opinion that it represents merely an abraded specimen of the type species. Donisthorpe's specimen was taken when beating elm in Windsor Forest on June 6th, 1935.

(*b*) FRUIT LEAF WEEVIL (*Phyllobius argentatus* L.). This weevil is abundant on apple, pear, plum and nut, and in addition it feeds on several kinds of soft fruits. It is also common in the nursery, infesting rootstocks, young trees, etc. in the spring.

It is curious that the occurrence of this very common species does not appear to be recorded in the economic literature of this country, since it must certainly be regarded as the most abundant green leaf weevil of the orchard and nursery.

It should be mentioned that there are two forms of this species. The type form is *P. argentatus* L., which has dark legs. It is accompanied by an aberration known as *P. argentatus* ab. *viridans* Boh., which may be distinguished at once by its pale yellow legs. The aberration is sometimes as numerous as the type form.

(*c*) COMMON LEAF WEEVIL (*Phyllobius pyri* L.). The common leaf weevil occurs on most kinds of top and soft fruit, but is more plentiful on pear, plum and damson than on others. It also feeds on many woodland trees and shrubs, including hazel, birch, etc. It is also abundant on nettle in June.

(*d*) Green Leaf Weevil (*Phyllobius maculicornis* Gm.). This leaf weevil has been regarded as the commonest fruit species for many years past, in fact Whitehead (1888) refers to it in his "Report on Injurious Insects" published in 1888. He states that it occurred in hordes in the orchards in 1887, devouring the petals and foliage of the fruit trees.

Theobald (1909) also refers several times to this species, and mentions the ravages caused by it to fruit trees in different parts of the country. There is little doubt, however, that both Whitehead and Theobald really refer to *P. argentatus* L., which has been persistently the commonest fruit tree species in Kent for many years past.

The specimens in Theobald's economic collection under the name of *P. maculicornis* Gm. proved to be *P. argentatus* L., and this tends to support the view that the species were not diagnosed accurately in the field.

The writer has occasionally found *P. maculicornis* Gm. in derelict apple orchards, especially on trees in the outside rows, where the branches frequently intermix with those in the adjacent hedgerows. A likely explanation is that the weevil has wandered from the hedge plants to the apple in search of fresh food. In captivity the weevil feeds more naturally on scrub oak than on apple foliage.

The natural food plant of this weevil is oak, and it is very partial to the cut-down scrub oak. It appears a little later in the season than other species of the genus, and is not commonly found until June.

(*e*) Leaf Weevil (*Phyllobius calcaratus* F.). The normal host plant of this weevil is alder, but it is found locally common on black currant in some parts of Kent. It has not been noted on other kinds of cultivated fruits.

It does not occur on black currant in large numbers and cannot be regarded as an insect of economic importance. It is of local distribution on alder, but is usually quite abundant where it occurs.

Another British species of Phyllobius which occurs commonly in Kent is *P. pomonae* Ol. It is found on oak, but in spite of its name it is not associated with cultivated fruit.

The genus Polydrosus is very closely allied to Phyllobius, and although all the species contained therein are leaf-eating, none of them infests fruit. One species, *Polydrosus cervinus* L., very occasionally feeds on the foliage of wild crab apple; but this appears to be an exception.

The British species of Phyllobius may be distinguished as follows :—

1. Brown; elytra without scales .. .. *oblongus* L.
2. Coppery or yellowish-green; elytra with scales; legs red.
   (*a*) elytra coppery; legs compressed (5-7 mm.) .. *pyri* L.
   (*b*) elytra yellowish-green (7-10 mm.) .. .. *calcaratus* F.

3. Green ; elytra with scales.
   (*a*) elytra with long erect hairs ; antennae entirely reddish (5-7 mm.) .. .. *argentatus* L.
   (*b*) elytra with very short erect hairs ; antenna, apex and scape dark (4-6 mm.) .. .. .. *maculicornis* Gm.

SUMMARY.

A short account is given of the five species of leaf eating weevils (*Phyllobius*) associated with cultivated fruits trees in Britain, viz. *P. oblongus* L., *pyri* L., *calcaratus* F., *argentatus* L., *and maculicornis* Gm., *P. pomonae* Ol., found on oak, and *Polydrosus cervinus* L., which very occasionally feeds on wild crab apple leaves, are also alluded to.

A key for the identification of the species that attack fruit tree leaves is supplied.

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OBSERVATIONS ON THE EFFECT OF POTASH SUPPLY ON THE TENSION OF THE TRACHEAL CONTENTS IN FRUIT TREES AND BUSHES

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Wallace (2, 3, 4) has shown that in the absence of an adequate supply of potash, the leaves of fruit trees develop "leaf scorch". An apical or marginal withering of the foliage, similar to leaf scorch, and associated with a deficiency of potash has also been recorded for a variety of plants other than fruit trees (7). It has been assumed that the leaf scorch develops as the result of an internal water deficit in the trees grown under potash-deficient conditions (6) and that potash-deficiency results in a state of physiological drought within the plant.

Observations on the water relations of potash-deficient trees refer mainly to experiments on cut shoots. Mann (1) investigated the transpiration rates of cut shoots of fully manured and potash-deficient apple trees, and the author (10) has demonstrated that the water conductivity of the shoots is—in proportion to the area of foliage carried—lower in potash-deficient than in completely manured trees. In the present paper data are presented which refer to the relative tension existing in the tracheæ of apples, gooseberries and raspberries, growing in the field, both under conditions of potash-deficiency and complete manuring. They are interpreted to mean that, under conditions favouring fairly high transpiration, an internal water deficit develops to a greater extent in potash-deficient plants than in plants under a system of complete manuring. It has long been known that even with a good water supply to the roots, tension develops in the tracheæ of plants when the conditions favour a relatively high transpiration rate, and that usually the tension disappears if the plant is exposed for long periods to conditions under which transpiration is nil. The existence of tension is taken to indicate the existence of a slight internal water deficit in the plant, and under certain conditions the magnitude of the tension may be a measure of the intensity of the water deficit.

Experimental.

(1) *Material.*

(*a*) *Apples.* Observations were made on trees of the variety Lane's Prince Albert growing on Malling II stock.

The trees were planted in December, 1932, and the observations made in September, 1938. The trees have been under a system of arable cultivation and manures have been applied each year as under :—

	Complete fertilizer plot cwt. per acre.	No potash plot cwt. per acre.
Nitrate of soda	2	2
Superphosphate	3	3
Sulphate of Potash	3	0

There was an obvious response to the potash, and the no potash trees exhibited typical leaf scorch.

(*b*) *Gooseberries.* The gooseberries used were of the variety Keepsake. They were interplanted between the Lane's Prince Albert apples referred to above and so received the same manurial treatment. Again, the no potash plants showed typical symptoms of potash deficiency.

(*c*) *Raspberries.* The raspberries used were of the variety Lloyd George. They were planted in the autumn of 1932 and the observations were made in September, 1938, on new canes which had developed during that year. The response of the raspberries to the manurial treatment has been described by Wallace (5). Each year since planting, both the complete fertilizer and the no potash plot have received nitrogen at the rate of 50 lb. per acre, and phosphate at the rate of 120 lb. of total phosphate per acre, whilst the complete fertilizer plot has received in addition annual dressings of sulphate of potash equivalent to 100 lb. of potash (K_2O) per acre. Symptoms of potash-deficiency were marked on the no potash plot and some leaf scorch was present.

(2) *Method.*

The method used for obtaining an estimate of the relative tension of the tracheal contents consisted in fixing a small plasticine cup around the shoot to be tested, filling the cup with a 1 % solution of acid fuchsin and stabbing the stem with a sharp knife beneath the surface of the dye solution in the cup. When this is done the red solution immediately enters the tracheæ, and travels a considerable distance both up and down the stem if the tracheal contents are in a state of tension, as they usually are when transpiration is active. The extent of this immediate dye penetration was taken to be a measure of the tension existing in the tracheæ before the stabbing of the stem. Only upward penetration of dye in the stem was determined (by rapid sectioning above the cup and examination with a hand lens) as it was not possible to determine downward penetration owing to contamination of the outer surface of the stem below the cup, caused by spilling the dye solution. With the apples, the plasticine cups were fixed to three or four year old shoots ; with the gooseberries, at the bases of the main branches ; with the raspberries, near the bases of the new canes.

Results.

The results obtained are incorporated in Table I. For each set of material it was possible to make determinations on a single occasion only, but each value given represents the mean of twenty observations, and the standard errors of these means have been calculated. To avoid as far as possible the introduction of errors due to any drift in the magnitude of the tension with time whilst the observations were being made, determinations were made alternately on complete fertilizer and no potash material. No evidence of any such drift in time was obtained and probably this precaution was unnecessary. Data referring to the weather conditions prevailing at the time the observations were made are given. All the observations were made in the afternoons of September 6th, 7th and 8th, 1938.

Table I.

Material.	Upward penetration of dye in cm. Mean values ± Standard errors.		Temperature °C.	Humidity %	Weather.
	Complete fertilizer.	No potash.			
Apples .. .. .. var. Lane's Prince Albert.	9·07 ± 0·81	13·08 ± 0·73	19·2	76	Bright sun and breeze. Rain a.m.
Gooseberries .. .. var. Keepsake.	5·98 ± 0·24	7·95 ± 0·41	19·3	74	Bright sun and practically no wind.
Raspberries .. .. var. Lloyd George.	8·86 ± 0·40	12·04 ± 0·50	19·4	70	Bright sun and practically no wind. Some drizzle a.m.

From the figures in the Table it will be seen that with each type of material the dye penetration was significantly greater in the no potash than in the complete fertilizer plants, and this is taken to indicate that under the conditions prevailing when the observations were made, a greater tension existed in the tracheæ of the no potash plants than in those of the trees and bushes receiving a complete fertilizer.

Discussion.

Under conditions of good water supply and minimal transpiration the tension existing in the tracheæ during periods of high transpiration tends to disappear, and the existence of tension can probably be taken to indicate a slight internal water deficit in the plant. Any tension, however slight, will tend to restrict the flow of water from the tracheæ to the evaporating surfaces of the leaf. The tension may have no serious consequences to the plant. Such tension

facilitates the passage of water from the soil to the tracheæ of the root but, as just stated, it hinders the flow of water from the tracheæ to the evaporating surface and so tends to reduce the amount of water lost by transpiration from the leaves. So long as the suction force of the tracheal contents does not exceed the maximum suction force which can be exerted by the non-flaccid living cells of the leaf there will be no flow of water from the living leaf cells back to the tracheæ. Under these conditions the living leaf cells can retain their turgidity. Manifestly, as the suction force of the tracheal contents increases, the living leaf cells will have increasing difficulty in maintaining a turgid condition unless the high suction force of the tracheal contents is compensated for by the ability of the leaf cells to develop a higher suction force. The suction force of the living leaf cells is due mainly to the presence of osmotically active substances in solution in the vacuoles, and the osmotic pressure of the vacuolar solution is probably a fair measure of the suction force which can be exerted. Many species of plants which show a tendency to develop a high tension in the tracheæ during periods of high transpiration also possess cell sap with a high osmotic pressure. Under these conditions a high value for the tension does not necessarily indicate an approach to a critical condition of internal drought. With the fruit trees and bushes to which the data presented here refer the position is different. There is no evidence that potash deficiency induces an increase in the osmotic pressure of plant cell sap. So far as the available evidence goes the reverse appears to apply (8). This being so it is probable that the increased tension of the tracheal contents brought about by potash-deficiency does indicate a more marked condition of internal drought and a nearer approach to the point at which internal drought becomes a critical factor in the tree's economy. Hence it is probable that in the no potash material this critical point is likely to be reached much earlier than in the complete fertilizer material. The reasons for this may be many, but two suggest themselves at once: (1) the increased stomatal frequency caused by potash deficiency (8, 10), which may be the cause of the increased transpiration found by Mann (1) in cut shoots from potash-deficient apples, and (2) the poor root development which may characterize potash-deficient plants (9).

ACKNOWLEDGMENTS.

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THE MIGRATION OF THE STRAWBERRY APHIS *CAPITOPHORUS FRAGARIAE* THEOB.

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Importance of the Strawberry Aphis.

In recent years commercial stocks of strawberry plants have become widely infected with certain virus diseases, described by Plakidas (1926, 1927) and Harris (1933) as Xanthosis (or Yellow-edge) and Crinkle. These diseases, which cause very considerable losses to the strawberry-growing industry, were proved by Massee (1935) to be transmitted by the aphis *Capitophorus fragariae* Theob. The wingless aphides in all stages of growth and the adult winged forms have been shown to transmit the viruses (Massee 1940). In the field, the spread of disease from plant to plant is entirely due to this aphis, and the elimination of this vector is the obvious way to control the diseases. Work on this problem has been in progess for some time and success has recently been achieved by the use of vaporised nicotine (Massee and Greenslade, 1939).

Life History of the Aphis.

Capitophorus fragariae can exist throughout the year in the form of apterous viviparous females on the strawberry plant. Other forms, though contributing to its importance as a pest, are not essential to its existence, and Hodson (1937) refers to 20 consecutive viviparous generations having been produced without reduction of fertility or in size of individuals.

The winter is passed on the under side of the older leaves in the angles between the veins, and by spring only partly grown nymphs are present. Living aphides were found in January 1940 on plants that had been completely buried in snow for over a month and had survived a partial thaw followed by freezing. During this time the ground temperature had fallen as low as $-5°$ F. and yet 2 out of 39 *Capitophorus* nymphs were found to be alive and became active at laboratory temperature. The population was so reduced, however, that normal numbers were not reached in 1940 until September, and no alatae were found in spring. Breeding normally begins in late March or April, and the population increases rapidly until late May or early June, when as many as 90 individuals may be counted on a single leaf. At this time a large proportion of the aphides develop wings. The population then declines until August when very few aphides can be found. In September, breeding becomes more rapid again, and a second high level of population is reached in October and maintained until falling

temperature reduces activity in December. Alate aphides appear again in autumn, but unlike the spring generation, they occur in small numbers over a long period. Sexual forms have been observed in January and February (Hodson 1937 ; Massee, Greenslade and Duarte 1938), but they are rare and are apparently quite unnecessary for the continued existence of the species.

The life cycle of *Capitophorus fragariae* shows a certain similarity to that of the Woolly Apple Aphis, *Eriosoma lanigerum.* Both species can exist through the winter as nymphs, and the egg has become an unnecessary part of the life cycle. In both cases suppression of egg production has proceeded to the same extent, that is, sexuales rarely occur, and although eggs are laid, the resulting fundatrix seldom establishes itself. The similarity in life cycle may be due to the fact that both species can feed during the winter whenever the temperature is high enough, since *E. lanigerum* is a bark feeder and *C. fragariae* lives on an evergreen plant. The winter leaves of strawberry have short petioles and are often pressed against the ground, while *E. lanigerum* lives in cracks in the apple bark. Thus, both habitats are protected from undue cooling by wind, and when there is any sun the temperature must often rise sufficiently high to permit feeding by the aphides.

Dates of Appearance of Alate Generations.

No definite date can be laid down for the appearance of winged aphides as this is naturally subject to seasonal influences. At East Malling the spring alate generation appeared in 1936 on May 13th, in 1937 on May 29th, and in 1938 on June 8th. Daily inspection of the strawberry fields enables the first and last date of appearance of adult alatae to be determined with some certainty, but the date of their appearance cannot be forecast from the condition of the plants. Table I shows the dates of flowering of Royal Sovereign strawberries at East Malling and the date of occurrence of the first winged aphides for the 4-year period 1936-1939.

Table I.

Dates of Flowering of Strawberries and of First Appearance of Winged Aphides.

	1936.	1937.	1938.	1939.
First flowers	May 8	May 8	April 11	May 4
Full bloom	May 21	May 24	May 20	May 23
Last flowers	June 8	June 5	June 6	June 3
First winged aphides	May 13	May 29	June 8	—

The flowering period was at approximately the same time in each year but the winged aphides must be looked for at any time from the beginning of May onwards. In 1937 and 1938, the adult winged aphides were seen for one week

only, but during this time they migrated to every strawberry plot on the Research Station farm ; in addition, experimental plants became infested even inside certain glasshouses the side lights of which were left open. The subsequent severe outbreak of virus disease all over the farm, which made very careful roguing necessary during the rest of the summer, was sufficient demonstration of the importance of this generation of aphides. In 1939 nymphs of the alate form were observed in a sheltered spot as early as April 28th, but in spite of daily search of infested plots only three adults were found and these on different parts of the farm on May 22nd. That some migration did occur in 1939 was shown by the fact that certain isolated plants known to be free from aphides in the spring became infested in June, but this migration must have been very slight. It is probable that a very few alatae were produced at intervals during the whole of May and that there was no considerable winged generation as there had been in previous years. Strawberry aphis was comparatively scarce in Kent in the early part of 1939. This apparent absence of the winged generation after nymphs had been seen was also noted in that year in Harpenden and in Northern Ireland by Messrs. C. T. Gimingham and R. Chamberlain respectively.

The autumn winged forms appear in much smaller numbers and over a longer period. In 1937, the first adults were seen on October 22nd and they continued to be found into November. In 1938, the first were seen on October 18th and some were still about on December 10th. Evidently alatae were produced in more than one generation during these months. In 1939, they were less numerous, only a few being noted, in mid-November.

Under laboratory conditions the winged forms of *Capitophorus fragariae* appear at any time in fair numbers, but in the field they are almost entirely restricted to the two periods mentioned above. A single nymph of the alate form was observed, however, at East Malling on July 27th, 1937, and it is possible that under exceptional conditions alatae may appear in numbers at other times.

Effect of Weather on the Flight of Winged Aphides.

The effect of weather conditions on the flight of aphides is most important. Davies (1935, etc.) has shown that *Myzus persicae* will fly readily only when the temperature is above 60° F., the relative humidity below 70 per cent. and the wind speed less than about $3\frac{1}{2}$ miles per hour. It is probable that extensive migration of *Capitophorus fragariae* takes place under similar conditions though no doubt some flight can occur under more rigorous ones. Thomas (in litt.) reports this species as taking flight in a fairly strong wind in May 1938. Observations made on some 300 autumn produced alatae in 1938 are given in Table II. The aphides were reared on a pot plant in a muslin sided cage and the conditions in it were recorded but not controlled. Light intensity was measured with a

Weston photo-electric exposure meter as used in photography. The observations were made over a two-day period.

The observations recorded in Table II are arranged in order of increasing activity of the aphides and not in the order in which they were made. It will be seen that flights took place at 61° F. and above. It was obvious, however, that light intensity had an effect apart from that of temperature. Considerable differences in activity were noted between the several observations made at 61° F. even between those made under the same degree of relative humidity. In one case the aphides were more active at 61° F. than at 70° F. In these observations it was, of course, impossible to separate completely the

TABLE II.

Temperature, Light Intensity and Activity of Alate Capitophorus fragariae.

Temp. °F.	Activity of aphides.	State of sky.	Light intensity, ft. candles.	Relative humidity %
55	No movement	Overcast	10—12	—
61	Few moving, no flights	Dull, raining	13	69
61	Some moving, no flights	Dusk, overcast	—	64
61	All moving, few short flights	Dull	30—32	65
61	All moving, few short flights	Sun visible through mist	50—60	69
59	All moving, few short flights	Sun visible through mist	50—65	—
70	Active, flying fairly freely	Sun and cloud	150—160	61
64	Active, flying freely	Sun visible through mist	160	61
61	Active, flying freely	Sun visible through mist	280	64
64	Very active, flying freely	Sunny	500	—
72	Very active, flying very freely	Sunny	400—650	62
69	Exceedingly active, continuous, sustained flights	Sunny	650—1000	58

effect of the three factors: light, temperature and humidity, and the lack of winged forms in 1939 and 1940 made it necessary to postpone further experiments.

Weather Conditions during Migration Periods.

If, as seems probable, *Capitophorus fragariae* responds to atmospheric conditions in the same way as *Myzus persicae* does, it is of interest to examine the weather conditions prevailing when alate generations were present. This will show for what periods the conditions were suitable for general migration and, in particular, whether any autumn migration could occur. Observations in the field on the spread of both aphis and virus disease suggest that there is, as a rule, no autumn migration; but there have been doubtful cases in which virus symptoms have appeared in spring on plants known to have been healthy in the

previous summer. If these plants had become infected at the time of the spring migration, symptoms of virus disease would have become visible during the ensuing summer, and in the absence of these it has been assumed that the plants became infected in the autumn. The expression of virus disease symptoms is delayed in winter. Diagrams (Figs. 1-6) have been constructed to show the daily fluctuation of temperature, relative humidity and wind speed during the periods when adult alate aphides were observed on strawberry plants at East Malling Research Station. The curves were obtained as follows:

Temperature. The maximum, minimum and 9 a.m. temperatures were obtained from the meteorological screen, and the times at which the maximum and minimum were reached were determined from thermograph records taken in a wire gauze insectary. It was known that the time of occurrence of the maximum and minimum temperatures in the insectary corresponded closely with those out of doors although the actual maximum temperature in the insectary might be higher. The shape of the curve was deduced from the insectary records and the Beaufort weather records. The curves so constructed do not of course show small fluctuations due to passing clouds, but it is possible to determine approximately the number of hours during which the temperature was above 60° F.

Wind Speed. Continuous wind speed records were taken by a Dines anemobiograph. It is possible to tell when wind speed is below 3 miles per hour, though the actual speed is not accurately recorded at so low a figure. The speed indicator was out of action from October 29th to November 9th, 1937, so that no curve was constructed for the autumn migration period of that year.

Relative Humidity. This was calculated for the periods when the temperature was over 60° F. and the wind speed below 3 m.p.h.

From the figures obtained in this way it is possible to determine for what periods during the occurrence of each winged generation conditions were suitable for sustained flight.

It is evident that there were often only short periods during the existence of winged generations when conditions were suitable for mass flights. In the spring migration of 1937, for instance, adult winged forms were present on the plants for 8 days, but it was only on May 31st and June 2nd that wind speed fell below 3 miles an hour, relative humidity was below 70 per cent. and the temperature was above 60° F. (Fig. 1). In 1938, such conditions occurred intermittently for a total of above 70 hours, and during some of the periods migration was actually noted (Fig. 2). In 1939, when migration seemed to have failed, it will be seen that suitable conditions prevailed each day on May 21st to 24th, 26th, 27th, as well as on six days in the first half of June (Figs. 3 and 4); but during the first half of May the temperature was never high enough, and in

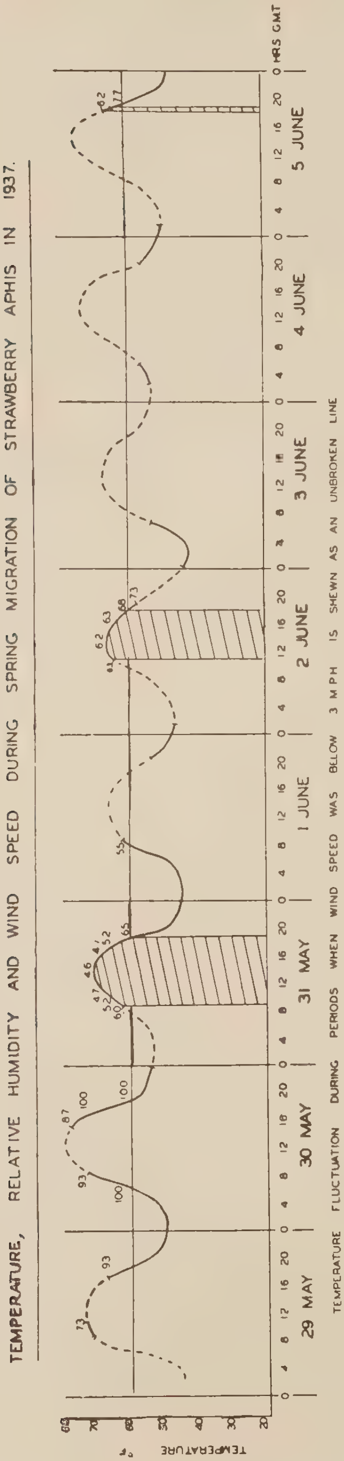
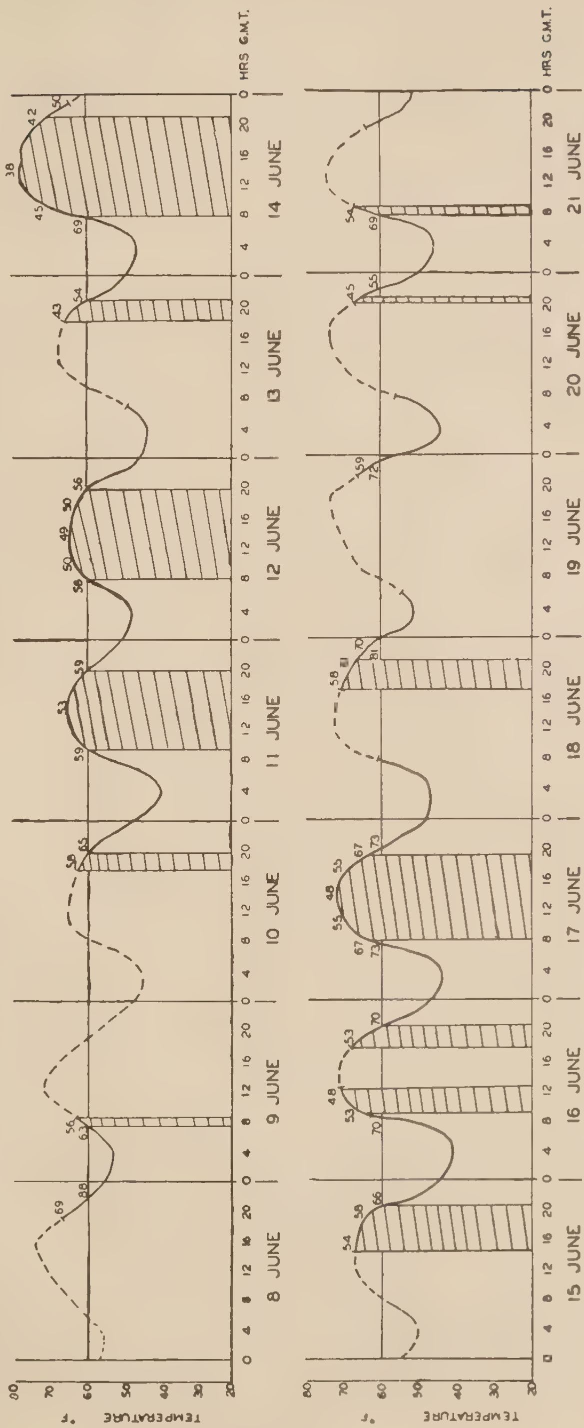

TEMPERATURE, RELATIVE HUMIDITY AND WIND SPEED DURING SPRING MIGRATION OF STRAWBERRY APHIS IN 1937.
TEMPERATURE FLUCTUATION DURING PERIODS WHEN WIND SPEED WAS BELLOW 3 M P H IS SHEWN AS AN UNBROKEN LINE
29 MAY
30 MAY
31 MAY
1 JUNE
2 JUNE
3 JUNE
4 JUNE
5 JUNE
HRS GMT
TEMPERATURE

FIG. I.



TEMPERATURE, RELATIVE HUMIDITY AND WIND SPEED DURING SPRING MIGRATION OF STRAWBERRY APHIS IN 1938.

FIG. 2.

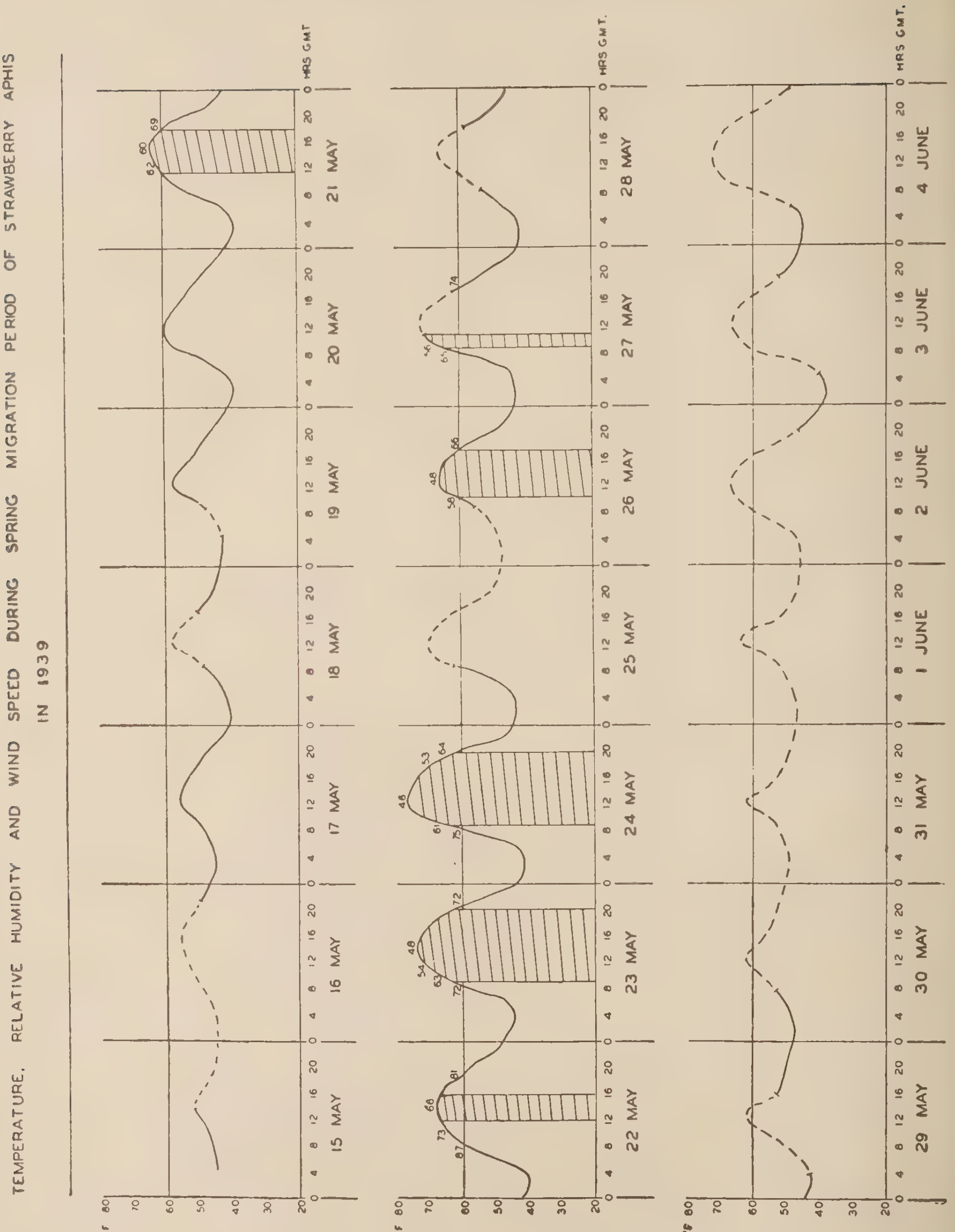

TEMPERATURE, RELATIVE HUMIDITY AND WIND SPEED DURING SPRING MIGRATION PERIOD OF STRAWBERRY APHIS
IN 1939
15 MAY
16 MAY
17 MAY
18 MAY
19 MAY
20 MAY
21 MAY
22 MAY
23 MAY
24 MAY
25 MAY
26 MAY
27 MAY
28 MAY
29 MAY
30 MAY
31 MAY
1 JUNE
2 JUNE
3 JUNE
4 JUNE
HRS GMT.
°F

Fig. 3.

TEMPERATURE, RELATIVE HUMIDITY AND WIND SPEED DURING SPRING MIGRATION PERIOD OF STRAWBERRY APHIS IN 1939.

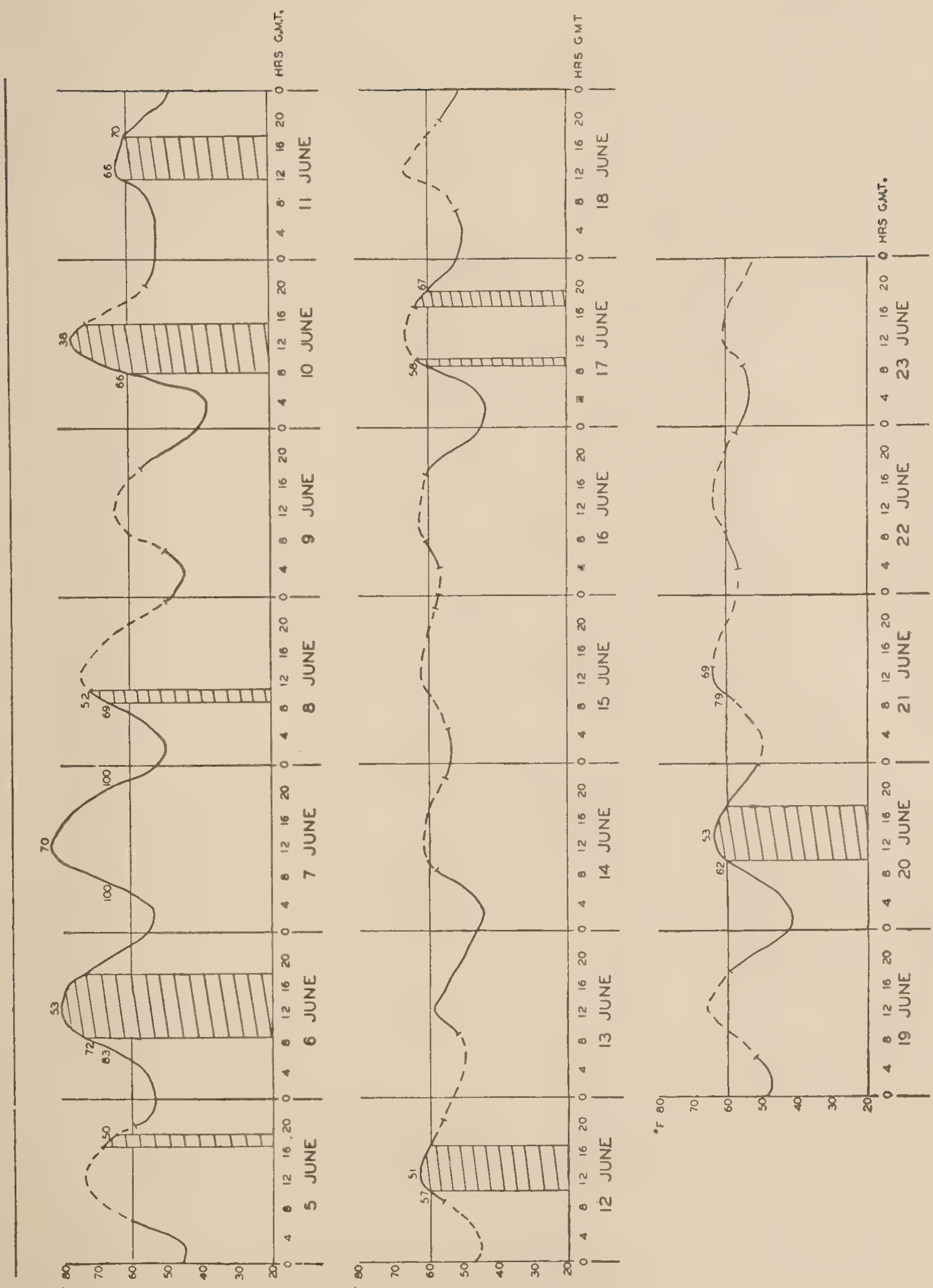
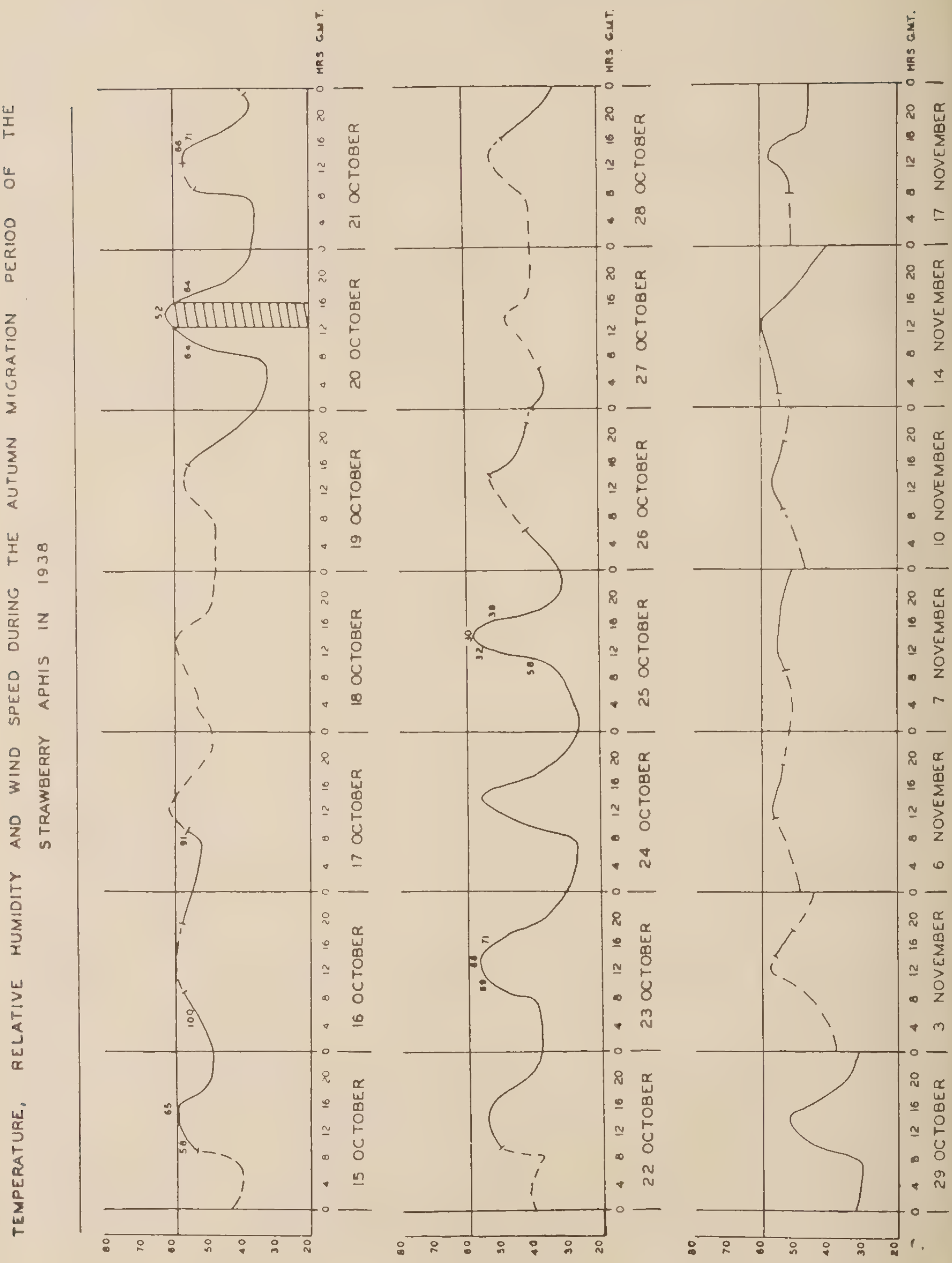


Fig. 4.



TEMPERATURE, RELATIVE HUMIDITY AND WIND SPEED DURING THE AUTUMN MIGRATION PERIOD OF THE STRAWBERRY APHIS IN 1938
HRS G.M.T.
15 OCTOBER
16 OCTOBER
17 OCTOBER
18 OCTOBER
19 OCTOBER
20 OCTOBER
21 OCTOBER
22 OCTOBER
23 OCTOBER
24 OCTOBER
25 OCTOBER
26 OCTOBER
27 OCTOBER
28 OCTOBER
29 OCTOBER
3 NOVEMBER
6 NOVEMBER
7 NOVEMBER
10 NOVEMBER
14 NOVEMBER
17 NOVEMBER

FIG. 5.

TEMPERATURE, RELATIVE HUMIDITY AND WIND SPEED DURING THE AUTUMN MIGRATION PERIOD OF STRAWBERRY APHIS IN 1939.

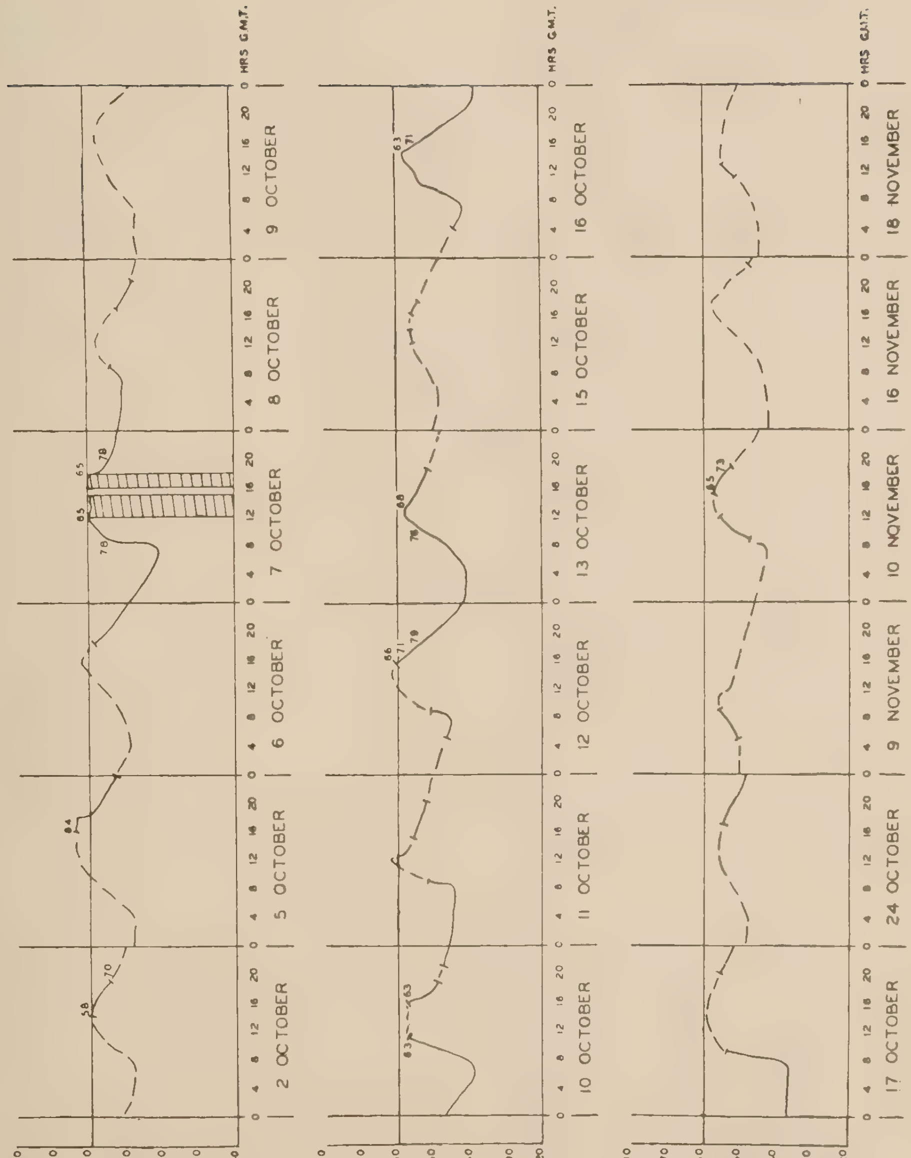


FIG. 6.

the first week of June there was too much wind. As mentioned above, a slight migration must have taken place in 1939, and it must have occurred on or after May 21st ; but in spite of daily search no alatae or their nymphs were discovered during this period, except the three previously mentioned, on the 22nd. Thus, very few can have matured at a time, as happens in the autumn, instead of large numbers, as usual.

In the autumn, adult alatae continue to appear in small numbers for six weeks or longer, but it has been considered that they do not fly, as conditions are rarely suitable. Examination of the temperature curves for October and November bears out this supposition. In 1938 (Fig. 5), the temperature rose only once above 60° F., on October 20th. Wind speed was then almost nil, and relative humidity was below 65 per cent. for a period of 5 or 6 hours, so that some migration could have taken place. In 1939 (Fig. 6), however, no such conditions prevailed after October 7th, which was before the usual time of maturity of the winged forms, so that general migration probably did not take place. In both years there were periods when the screen temperature was over 55° F. with the wind speed below 3 m.p.h. and relative humidity below 70 per cent., so that in a sheltered plot of strawberries the temperature may have been higher, allowing short flights from plant to plant. Similarly the recorded wind speed on November 5th, 1939 was above 3 m.p.h., yet flight of other species of aphides was observed in a sheltered spot on the North Downs. These short flights are not important, as the alatae would not by means of them carry the virus diseases farther than they had already been carried by the apterae which move from plant to plant in the summer. The important point is that weather conditions in autumn may very occasionally be such as to allow of migration to distant fields, and therefore the possibility of the introduction of virus diseases by means of the strawberry aphis to a healthy plantation at this season must be borne in mind. Harris (unpublished results) has noted cases of the appearance of virus diseases in strawberry plantations in May which can have occurred only by this means.

Colonization of Isolated Strawberry Plants by Alate Aphides.

In 1938 and 1939, experiments were carried out at East Malling Research Station to determine whether migrating alate *Capitophorus fragariae* could find and colonize isolated strawberry plants. It was hoped that at least partial answers would be obtained to three questions : (1) How does the migrating aphis find its foodplant ? (2) Can a few intervening garden strawberry plants act as stepping stones to enable aphides to pass from one large field to another some distance away ? (3) To what distance can this aphis migrate ?

Healthy Royal Sovereign strawberry plants, raised in an insect-proof house, were planted on March 11th, 1938 amongst other fruit crops and in odd

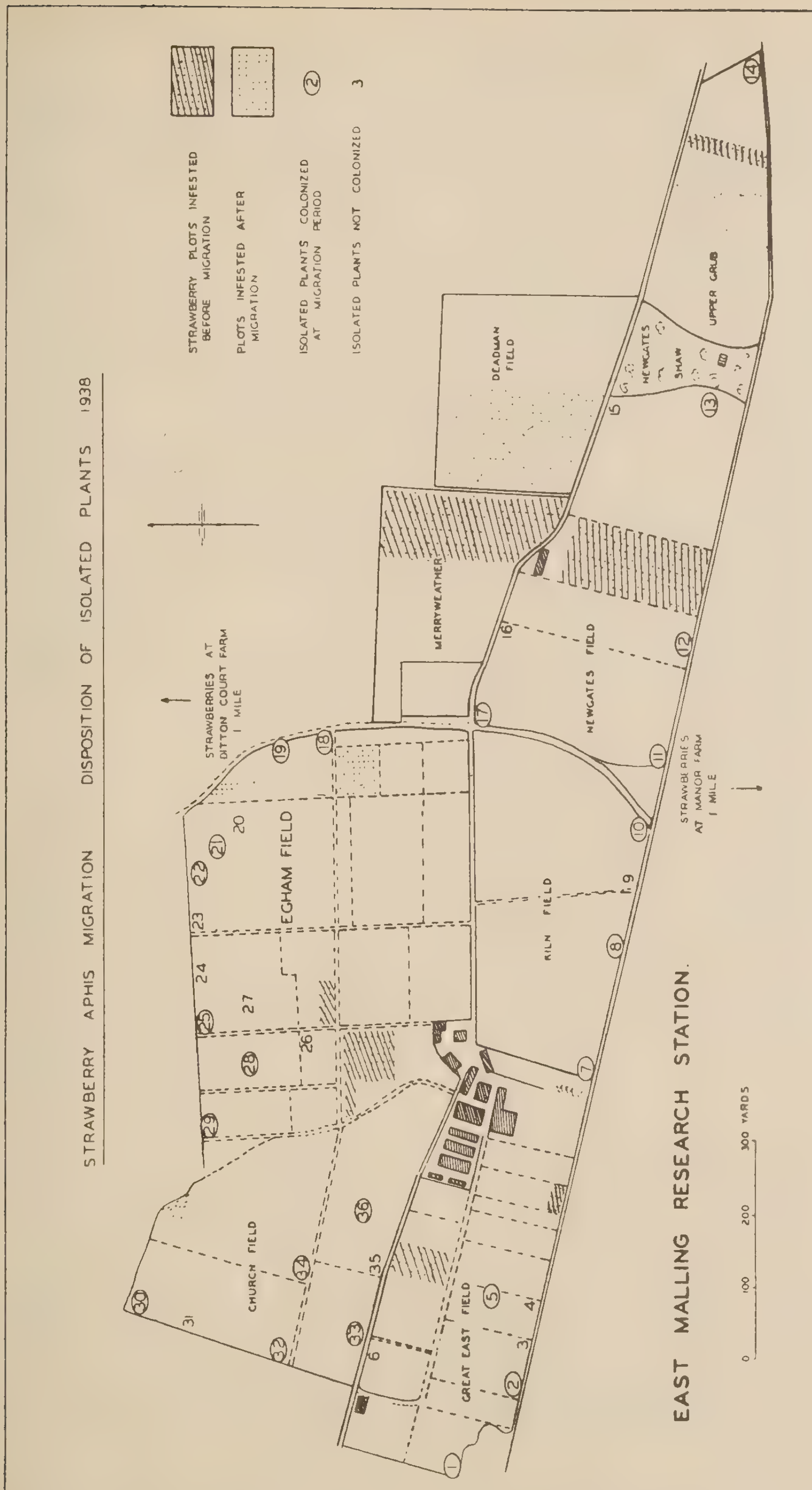

STRAWBERRY APHIS MIGRATION
DISPOSITION OF ISOLATED PLANTS 1938
STRAWBERRY PLOTS INFESTED BEFORE MIGRATION
PLOTS INFESTED AFTER MIGRATION
ISOLATED PLANTS COLONIZED AT MIGRATION PERIOD
ISOLATED PLANTS NOT COLONIZED
STRAWBERRIES AT DITTON COURT FARM 1 MILE
STRAWBERRIES AT MANOR FARM 1 MILE
DEADMAN FIELD
MERRYWEATHER
NEWGATES SHAW
UPPER GRUB
NEWGATES FIELD
EGHAM FIELD
KILN FIELD
CHURCH FIELD
GREAT EAST FIELD
EAST MALLING RESEARCH STATION.
0
100
200
300 YARDS

FIG. 7.

corners all over the Research Station farm, as shown in Fig. 7, which also shows the position of infested plots of strawberries. Weekly observations were made from the migrating period onwards, and on October 3rd, 26 out of 36 plants carried established colonies of aphides. The plants so colonized are marked on the plan. That migrating aphides could find an isolated plant among some other crop was thus established, as was the fact that small beds of strawberries could act as stepping stones between commercial fields. In other words, a garden plot at the maximum distance of migration from an infested field could become colonized by migrating strawberry aphides, and in the next winged generation a clean field further on could become infested in turn from the garden, although the two fields might appear to be sufficiently far apart from one another to prevent invasion. This is important, since the only practical way of raising virus-disease-free strawberries is to treat all the healthy young plants against aphis by dipping them in an insecticide and then to grow them at a considerable distance from other strawberries to avoid infestation by viruliferous winged aphides. Control of the aphis on established plants has been proved possible only recently by the use of nicotine vapour, which is quite widely used for other aphides in the United States. This method has been tested at East Malling and elsewhere (Massee and Greenslade, 1939; *Kent Farmers' Journal*, 46: 166), and is being developed by a commercial firm.

A similar experiment carried out in 1939 confirmed the fact that migrating strawberry aphides can find isolated strawberry plants, even among thick grass. In that year, as stated previously, only three alatae were found in May, and it seemed as if this winged generation had failed to develop, yet 6 out of 23 isolated plants became infested with strawberry aphides at the end of June and a further 5 did so after the autumn migration. The plants which became infested at that time lay between a high railway bank and a plantation of apples. Probably under such sheltered conditions the temperature rose sufficiently on windless days to allow the flight of aphides from a small infested plot of strawberries in the same situation, although conditions were not suitable for general migration in 1939.

Direction and Distance of Migration.

If migration takes place only when wind velocity is below 3 m.p.h. the dispersal of aphides should take place in all directions, not in any particular one. This was so. In 1939, for example, plants 250 yards east and 400 yards west of the source of aphides became infested at the same time. The maximum distance of migration observed in these experiments was 400 yards, but no doubt winged strawberry aphides can travel farther than that. Colonization of new strawberry plots, apparently by migrating aphides, at distances up to a mile from infested strawberries has been noted, but unfortunately without absolute certainty that the distant plants were free from aphides before the flight period.

Knowledge as to how far *C. fragariae* can migrate would, of course, be very valuable to the commercial strawberry grower wishing to start a new plantation in isolation from infested fields.

COLONIZATION BY APHIDES OF PLANTS IN DIFFERENT SITUATIONS.

The situation of the isolated healthy plants apparently made little difference to their colonization by *Capitophorus*. Plants under trees or in grass were discovered as readily as those in the open. Table III gives details concerning the infested and the aphis-free plants in 1938 analysed according to their situation.

The fact that some plants did not become colonized was almost certainly

TABLE III.

Effect of situation of Strawberry Plant on colonization by Capitophorus fragariae.

Situation of Plant.	Colonization after migration.		Not colonized.	
	Plant No.	Yards from infested plot.	Plant No.	Yards from infested plot.
Bare soil in open	1	250	15	150
	6	130	16	100
	11	200	26	20
	12	60		
	13	200		
	14	125		
	17	225		
	18	300		
	19	325		
	35	120		
	10 plants.		3 plants.	
Bare soil under tree or in hop garden	2	170	3	150
	7	30	23	190
	25	160	24	160
	28	100	27	90
	29	190	31	300
	30	390		
	32	175		
	33	100		
	34	15		
	36	60		
	10 plants.		5 plants.	
In grass	5	70	4	120
	8	220		
	9	300		
	10	300		
	4 plants.		1 plant.	
Under dense Trees	21	250	20	230
	22	200		
	2 plants.		1 plant.	

due to chance. No difference in conditions could be seen between the environment of the aphis free plants and that of some of the plants which became infested with aphides. Permanent colonies of aphides were not established on Nos. 28, 29, 30, 32, 33, 34, but these plants were small, possibly because all of them suffered from severe root competition from a poplar hedge, currant bushes and hops.

Selection of Host Plant by Strawberry Aphis.

There is little published evidence to show how aphides find their host plants and some observations made in 1938 illustrate the complexity of this problem. *Capitophorus fragariae* has never been found occurring naturally on wild strawberry, *Fragaria vesca*, yet it may easily be reared on wild strawberries in pots although never so freely as on certain commercial varieties. Pot plants differ from wild ones in several obvious ways. They grow in a compost different from their normal soil, they are not in competition with other plants, and since the runners are removed the plants make more growth than those under natural conditions. In order to ascertain whether any of these factors affected the aphis, some wild strawberries were planted in a clearing in a small piece of woodland, marked Newgates Shaw in Fig. 7. This has been uncultivated for 100 years or more and is now a chestnut coppice. Part of a plot of 20 feet by 10 feet was cleared and cultivated and part was left with a natural covering of wild plants including a thick growth of wild strawberries. Twenty wild strawberry plants were grown in the cultivated part, ten being allowed to make runners, and the other ten having their runners removed regularly so that they became large plants. At the same time the runners from some of the wild strawberries in the uncultivated part were removed. At the migration period, in June 1938, all the plants in the cultivated part of the plot had been discovered and colonized by winged strawberry aphides. The distance from the nearest infested field was 250 yards, including 20 yards of chestnuts, 10-12 feet high. A careful search of the wild strawberries growing in the grass, whether with or without runners, failed to reveal a single strawberry aphis on them, but two young plants about a foot inside the cultivated part and still joined by stolons to the parent plant in thick grass had both become colonized. In another part of the wood the ground had been cultivated around a newly planted young walnut tree, and in yet another place about one square yard of surface vegetation had been removed leaving bare soil. In each place there was a young strawberry plant infested with aphides and still attached to the uninfested parent plant in the grass.

It was evident that neither the woodland soil nor the removal of runners had influenced the aphis, though a difference was found between plants in natural conditions and those in the same soil but kept free of other plants. To

explain this, the way in which migrating aphides find their host plants must be considered. They may seek them out deliberately or they may come across them by mere chance. That is to say they may fly about until some stimulus is received which guides them to the plant or they may fly from plant to plant inserting the stylets in each until one is found to be a strawberry. If, as Profft (1939) suggests, aphides are guided to the plant by the sense of smell then it is possible that wild strawberries are attractive but not perceived by the flying insects. It is possible, for instance, that the odour of the plants in grass is disguised by that of the other vegetation, or that a rising current of warm air from the bare soil carries the odour to aphides flying above it, whereas air does not rise from the moister vegetation beside the cultivated plot. Cultivated strawberries, the preferred host plant, may have a stronger odour than *Fragaria vesca*, enabling them to be found in long grass. Against this must be set the fact that it has been impossible to establish *Capitophorus fragariae* on naturally growing wild strawberry plants in the field and that large patches of wild strawberries would certainly have been discovered by chance. If, on the other hand, aphides find their host plants by chance then they must find wild plants in the grass but fail to establish themselves on them. This cannot be due to any micro-climatic conditions, as cultivated strawberries planted in similar positions are readily discovered. It is just possible that natural vegetation harbours more predators than a strawberry field, but this again seems unlikely as there are always numerous predaceous insects and spiders in any strawberry field. A third possibility is that *Fragaria vesca* growing in natural conditions is actually distasteful to the aphides or unsuitable for their growth, owing to some chemical or physical difference in the sap.

An attempt was made to determine the effect of competing vegetation on cultivated strawberries by examination of plants in a neglected field rapidly being overrun by weeds. To avoid confusion due to uneven distribution of aphides in the field, plants were examined in pairs, every plant not in contact with weeds was examined and compared with an adjacent plant surrounded by weeds. Sixty-nine such pairs could be found, of which 13 had aphides on one of the plants. The aphides were present on the open plant in 7 pairs, on the weedy one in 4 pairs, and on both plants in 2 cases. These figures are sufficiently different to make further counts worth while when opportunity occurs, but it is probable that there is no real difference between the aphis population of plants surrounded by weeds and those in the open.

As no obvious explanation could be found for the lack of strawberry aphides on wild strawberry plants, experiments were carried out to determine whether the alate aphides can find their host plant by sense of smell. The apparatus used is illustrated in Fig. 8, Plate I. The winged aphides were placed in the hurricane lamp glass shown at the back of the retort stand which was connected by a papier-mâché Y tube to the two other lamp glasses resting on the

box. Strawberry leaves were placed in one of these and grass in the other. Air was forced into the box by a slow speed fan and passed out through muslin covered holes into the bottoms of the lamp glasses, thus providing a slow current of air taking the odour of the strawberry leaves and the grass into the glass occupied by the aphides. The air speed as measured by an Alnor velometer was 1 to 2 miles per hour. Relative humidity and air temperature were measured by placing wet and dry bulb thermometers above the lamp glasses as air was being blown through. A 250 Watt floodlight was placed in front of the two lamp glasses, and after inserting the aphides into the lamp glass at the base of the stand it was covered to keep out light. The aphides were thus attracted towards the light through the two branches of the Y tube, the air from each side being at the same temperature and relative humidity and moving at the same speed. After several hours nearly all of them were to be found in one or other of the two illuminated glasses. The following are the details of the results obtained :

	Time.	Temp.	Relative Humidity.	No. of aphides on strawberry.	No. of aphides on grass.
1st Experiment ..	23 hrs.	—	70%	6	0
2nd Experiment ..	2 hrs.	70° F.	30%	14	26
3rd Experiment ..	2 hrs.	60—80° F.	68—48%	17	13
4th Experiment ..	5 hrs.	60—80° F.	68—48%	10	8

In the 3rd and 4th experiment the flood light was placed closer to the lamp glasses than before and this was responsible for the rise in temperature between the beginning and end of the experiments. The total numbers of aphides going to strawberry leaves and to grass were equal, which suggests that the odour of the leaves did not affect their choice of direction. These experiments were carried out, however, with autumn alatae, and it is just possible that the spring generation might react differently.

The absence of *Capitophorus fragariae* from wild strawberries is not yet explained but the available evidence suggests that these plants are in some way distasteful to the insect, which will not therefore remain on them.

SUMMARY.

The life history and economic importance of the Strawberry Aphis, *Capitophorus fragariae* Theob. are briefly discussed and the main part of the paper deals with the behaviour of the winged generations. In nature, the aphis is practically confined to the cultivated strawberry plant. Winged generations occur, but they serve merely to spread the species. There is no migration to an alternate host. [This aphis, however, has been found very rarely on *Potentilla*

anserina.] The winged generations are economically important because they spread strawberry virus diseases from field to field. The spring alate aphides are adult for a short period in May or June and often occur in very large numbers. Their occurrence is not correlated with the flowering period of the plant. The autumn alatae, on the other hand, are less numerous and occur over a longer period.

The activity of winged aphides is known to be influenced by temperature and humidity, and evidence was obtained of the influence of light. Charts showing the temperature, relative humidity and wind speed prevailing during the time of production of the winged generations are reproduced and show that extensive migration is likely to occur only during comparatively short periods. They also show that extended migration of the autumn winged aphides is unusual but can sometimes occur, and that the transmission of virus disease at that season is therefore possible.

Migrating strawberry aphides are able to find single strawberry plants among other crops or among thick grass. They fly in all directions and cannot be much affected by the direction of the wind since they do not fly unless the wind speed is very low. Plants become infested at distances of at least 400 yards from infested plots of strawberries, and there is little doubt the aphides can migrate farther than this.

Wild strawberry plants growing under natural conditions do not become colonized by strawberry aphis, although cultivated plants growing under exactly similar conditions readily become infested. Under certain unnatural conditions wild strawberry plants may support large colonies of the aphis. The possible reasons for this are discussed and experiments are described which suggest that a sense of smell is not concerned with the choice of a host plant by this aphis.

ACKNOWLEDGMENT.

The writer is greatly indebted to Dr. I. Thomas for permission to refer to his unpublished observations on Strawberry Aphis and for valuable criticism of this paper before publication.

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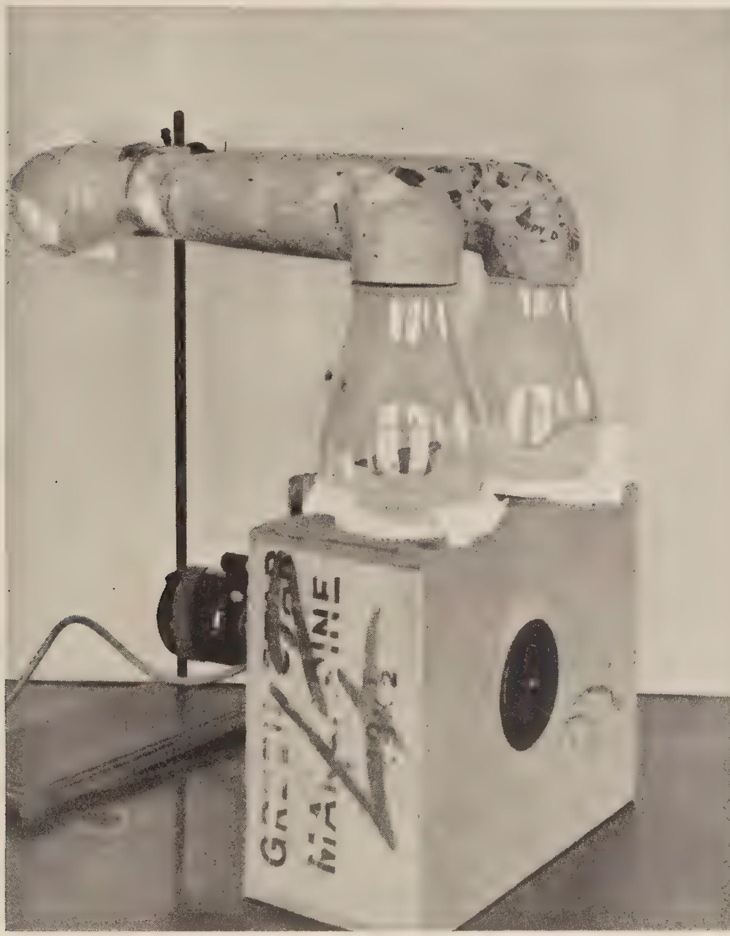

Fig. 8.

Apparatus for testing the response of Strawberry Aphis to the odour of the food plant.

PLATE I.

Fig. 1.

Early symptoms caused by Cucumber Virus No. 1, viz. faint spikiness of the leaves and absence of mottle.

Plant inoculated 29/3/1940. Photo 1/5/1940.

Fig. 2.

Later symptoms of disease caused by Cucumber Virus No. 1, viz. narrow, distorted leaflets. Foliar mottling is absent.

FIG. 3.

Plant inoculated with Tomato Mosaic Virus, Strain A.17, showing dark-brown stem lesions.
Plant inoculated 29/3/1940. Photo 12/4/1940.

FIG. 4.

Plant inoculated with Tobacco Virus No. 1, showing light-brown stem lesions and foliar necrosis.
Plant inoculated 29/3/1940. Photo 12/4/1940.

PLATE III.

Fig. 5.

Undersides of leaflets of plant inoculated with Tomato Mosaic Virus, Strain A.17, showing small enations and laminar distortion. Foliar mottle is absent.
Plant inoculated 29/3/1940. Photo 1/5/1940.

Fig. 6.

Marginal enations of a leaflet of a plant inoculated with Tomato Mosaic Virus Strain A.17. There is a faint foliar mottle.
Plant inoculated 29/3/1940. Photo 20/8/1940.

THE EFFECTS OF CERTAIN MOSAIC-INDUCING VIRUSES ON THE TOMATO CROP UNDER GLASS

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INTRODUCTION.

In the British Isles the commercial tomato grower distinguishes three or four of the common virus diseases of this crop under the names of Streak (Stripe), Mosaic and Spotted Wilt. Of these, Spotted wilt is almost invariably confined to mixed nurseries, where the virus is carried to the tomato from one of its numerous bedding-plant or other hosts. These designations cover all the serious outbreaks of tomato virus disease under glass in this country, and experience has shown that 95% of the virus problems encountered in large tomato nurseries may be attributed to the Tomato Mosaic Virus (Bewley, 1922) and Tobacco Virus No. 1 (Johnson).

The work of Ainsworth (1933, 1935, 1937) and others has indicated that there are probably several distinct virus entities included in the Mosaic-inducing group, in addition to the virulent mixtures of potato and tomato viruses causing Mixed Virus Streak. It is not the purpose of the present paper, however, to discuss in detail the several virus diseases of the tomato that have been described and the specific viruses believed to be responsible for them, for the aim of the work now to be described was to determine the effects of certain widespread Mosaic-inducing viruses on the yield and quality of tomato fruit produced on plants grown as nearly as possible under the conditions of nursery practice, and also to investigate the causes to which any reduction in fruiting might be attributed.

Design of Experiment.

The experiment was designed to investigate the effects of infection with four viruses on the growth and yield of a tomato crop, but difficulties were experienced in the full execution of the original plan, and these will be dealt with as they arise.

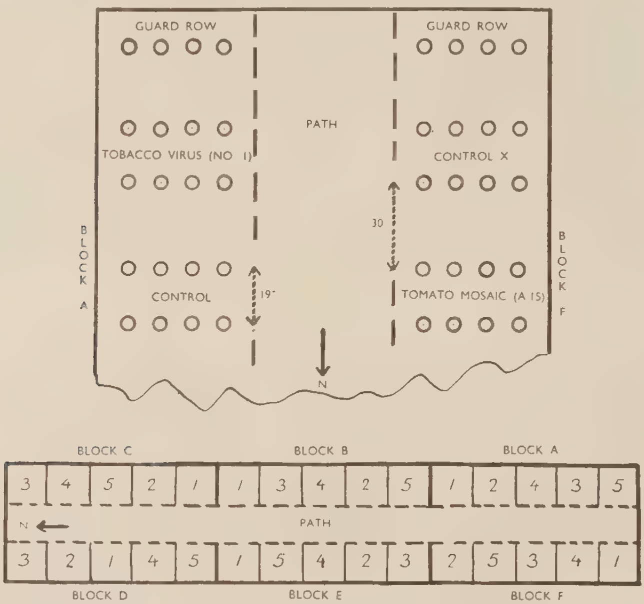
A cucumber house, 70 feet by 13 feet, was used, representing an effective area of approximately $\frac{1}{81}$ acre. This was divided into six blocks, each containing five plots distributed at random within the blocks. Each plot contained eight plants, making a total of 240 plants in all. The lateral spacing was 19 inches between plants in the plots and 30 inches between the plots. At this rate of planting there would be 13,464 plants per acre. Reference to the plan in Fig. 1 will indicate the general lay-out of the house.

Treatments.

The four representative viruses mentioned below were selected for inoculation into healthy plants, the development of which was to be compared with that of similar but uninoculated healthy plants.

(1) *Cucumber Virus No.* 1 (J. Johnson). This virus was taken from tomato plants showing typical " fern leaf " symptoms, and when transferred to cucumber

PLAN OF EXPERIMENT



1 = CONTROL X
2 = TOMATO MOSAIC VIRUS (A.17)
3 = CONTROL
4 = TOMATO MOSAIC VIRUS (A.15)
5 = TOBACCO VIRUS No. 1

FIG. 1.

plants it induced a yellow mottle. The description given by Ainsworth (1935) was in agreement with the symptoms induced by this virus in young tomato plants. It was not found possible to infect successfully all the plants of this group of plots with the virus, a result which substantiates Ainsworth's work. No reliable data were obtained, therefore, concerning the effect of this virus on crop yield or growth. For completeness of variance analysis the data from this group of plots have been recorded as " Control X ". Some interesting symptom pictures were, however, obtained from the plants that did become infected with this cucumber virus.

(2) *Tomato Mosaic Virus* (Strain A.17). This virus was obtained in the summer of 1939 from a nursery at Worthing, Sussex, which had suffered severe crop reduction attributed largely to this virus. When transferred to *Nicotiana glutinosa* and *N. tabacum*, many coalescing local lesions were produced on the leaves of both species. In the latter, the disease became systemic, producing a mild, light and dark green foliar mottle. On seedling tomato plants a yellowish-green mottle was induced in the summer months and fern-leaf in the winter. A few infected plants had been noted with pale-brown stem streaks and necrotic spots on the younger leaves. On crop plants the symptoms produced by this virus agree with those described by Bewley (1922) for Mosaic disease of tomato, and in many respects they are similar to those figured by Westerdijk (1910) for tomato Mosaic disease. This virus is probably the same as that which causes the Single Virus Streak of Ainsworth.

(3) *Tomato Mosaic Virus* (Strain A.15). A brief description of the symptoms caused by this virus in the tomato has been given by the author (1939). It was obtained from a nursery in Sussex, where infected plants appeared to suffer no ill effects from the disease. Prior to the work reported in this paper, no case of stem streaks or leaf necrosis had been observed in tomato plants infected with this virus, and it was at first thought that a mild strain of tomato Mosaic virus had been obtained which might be used for protective inoculation. The present experiment has confirmed the relative mildness of this virus in its effect on the cropping capacity of the plant. On *Nicotiana glutinosa* and *Datura Stramonium* a few small local lesions were produced by it, and on *N. tabacum* a small number of local lesions were followed by systemic infection of the plant and the production of a very faint, pale-green leaf mottle.

(4) *Tobacco Virus No.* 1 (J. Johnson). This is believed to be descended from Johnson's original strain which came to Cheshunt some years ago via Rothamsted. The virus has been maintained here continuously on *N. tabacum*. The symptoms shown by plants inoculated with this virus have been described by Ainsworth (1933) for tomato seedlings, *N. glutinosa*, *N. tabacum* and *Datura Stramonium*.

There were eight uninoculated (Control) plants in each plot. Observing the simple, hygienic measures outlined below, it was possible to keep them free from symptoms of virus infection until the fifth truss was in bloom. For the first nine weeks of the experiment, therefore, all the Controls appeared healthy, but after this time infection gradually spread throughout these plants.

Inoculation and Prophylaxis.

Leaves containing the particular virus to be used for inoculation purposes were placed with a little distilled water in a mortar and finely pulped by grinding

with a pestle. The plants were inoculated by gently wiping one leaflet of each leaf on the plant with muslin soaked in the infectious juice. Inoculation was carried out ten days after planting out in the borders, when 10-12 leaves had developed and the flowers of the first truss were opening. It was deemed advisable to refrain from handling the Control plants at this stage, particularly as the method had been used many times on similar plants, with distilled water as inoculum, without detriment to the normal growth of the plant.

Throughout the course of the experiment no one but the author was permitted to handle the plants and the house was always kept locked. When tying, trimming, picking or measuring the plants, the plots for each treatment were always dealt with separately, and hands, knives and instruments were thoroughly washed with soap and water before beginning work on another series. During any one operation, the plants were handled in the following order, to reduce the risk of infection or cross infection to a minimum : (1) Control, (2) Cucumber Virus No. 1, (3) Tobacco Virus No. 1, (4) Tomato Mosaic Virus (strain A.15), (5) Tomato Mosaic Virus (strain A.17). The plots were 30 inches apart, and this helped to prevent contact infection between neighbouring plants.

On May 15th one plant of the Control series showed a virus mottling, but it was not until June 20th that all the Control plants were showing similar symptoms. Comparisons recorded below between infected and Control plants were thus between plants infected artificially with specific viruses when the first flower-truss was in bloom and plants that became accidentally infected with undefined Mosaic-inducing viruses when the fifth truss was in bloom. During the period in which leaf counts and height measurements were made, the Controls were all healthy.

Plant Material, Culture and Manuring.

Tomato seed of the variety Potentate, saved from virus-free plants, was sown on December 16th, 1939 in seed trays in sterilized maiden loam to which had been added a small quantity of lime, potash and phosphate. When the first two rough leaves had developed, the seedlings were transferred (on January 11th, 1940) to 3-inch pots containing old sterilized tomato soil supplemented with lime, superphosphate and a little stable manure. The plants were transferred to the borders on March 19th, 1940, when 8-9 foliage leaves had emerged. They were inoculated on March 29th and the first heavy watering was given on April 25th, 1940.

The plants were staked and then trained on strings until the sixth flower truss had been produced. Those in the front three rows of each plot were then stopped, and those of the back or wall row were allowed to grow up to the glass

roof so that any symptoms produced late in the season might be observed. Side shoots were removed from all plants every ten days.

Watering was carried out freely as soon as the first truss had set, and overhead damping to facilitate fruit setting was done according to the recommendations of Bewley (1938). The mean weekly air temperatures are shown in Fig. 2. The maximum temperature recorded was 102° F. and the minimum 50° F. At night the temperature rarely fell below 58° F. and the average day and night temperature for the duration of the experiment was 71·1° F. Potentate is a variety used for early crops and responds well to

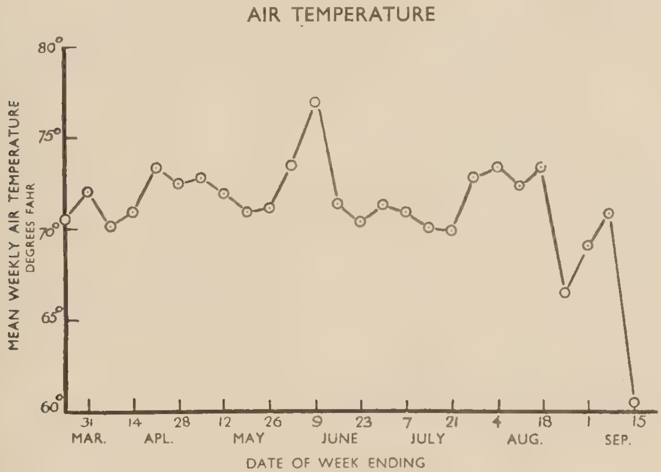


FIG. 2.

temperatures rather higher than those normally recommended for the culture of varieties such as Ailsa Craig, E.S.1, etc.

Routine fumigation was carried out, using nicotine shreds and tetrachlorethane, to control thrips and white fly respectively.

Soil.

The soil of the house was a rich loam in which tomatoes had not previously been grown. The top strawy residues of the beds previously used for cucumbers had been removed, but it was anticipated that the nitrogen content of the soil would be high. The standard base dressings of lime and potash were applied, but the nitrogenous base was omitted. Slaked lime was applied at the rate of two tons per acre and sulphate of potash at the rate of 10 cwt. per acre; the soil was lightly forked over before planting.

As this procedure had confidently been recommended as successful nursery practice, a soil sample was taken after applying the base fertilizers, sampling

with a trowel to a depth of 6-7 inches. The result of an analysis of the sample, calculated for soil dried at 100° C., was as follows:

Loss on ignition	15·99%	Total P_2O_5	0·796%
Total nitrogen ..	0·537%	Available P_2O_5	0·260%
Total K_2O ..	0·652%	Total carbonates as $CaCO_3$ ..	4·790%
Available K_2O ..	0·216%		

The analysis was very kindly undertaken by Dr. Owen of this Station, who stated that the total nitrogen was very high for a tomato soil (0·42% total nitrogen is generally considered to be high). There is, however, no satisfactory method for assessing the fraction of the total nitrogen that is likely to be available to plants, particularly when a high level of mineral nutrients is being maintained in the soil. From the appearance of the plants it was considered necessary to start top-dressings with nitrogenous fertilizers at the end of April, when the first fruit trusses were swelling. Murneek (1926) has pointed out that nitrogen starvation of the vegetative parts of the tomato plant may supervene when the plant is fruiting, quite independently of the level of the external nitrogen supply.

Top-dressings were continued at intervals throughout the season whenever the condition of the plants appeared to demand them. Mixed fertilizers were used, of which the most important constituents were dried blood, sulphate of ammonia, superphosphate and nitrate of potash.

During May a few plants showed symptoms of iron-deficiency chlorosis; this was quickly checked by the application of dried blood which, although not applied for that specific purpose, provided a useful source of readily available iron.

Winter flooding of the soil was inadvertently omitted, although this is a generally accepted practice in commercial culture.

The manurial treatments applied in this experiment and the soil analysis results have been presented in some detail for the following reasons:—

(1) In reports of work with glasshouse soils and especially in studies of virus diseases under glass, there exist many discrepancies which are, in the writer's opinion, to a large extent due to a failure to present even the elementary details of the nutrient composition of the soils used, thereby tending to make independent, confirmatory experiments almost impossible. It is regretted that it was not possible to include soil moisture measurements in the present study.

(2) Consideration of the soil used and the fertilizers applied will make it clear that soil nutrient deficiency was not likely to have been a factor seriously limiting the growth of the plants, and that the effects of the viruses have been investigated under such conditions as are likely to occur only on well-manured nurseries with loam soils. There are adequate empirical data available at this

Station to indicate that the severity of a virus disease in the tomato crop is greatly accentuated on badly managed or infertile soils. Thus, the results reported in this paper for crop reduction should not be presumed to represent necessarily the maximum loss which tomato growers might attribute to virus disease, nor should the symptoms recorded for these diseases be dissociated from the environmental factors operative, in so far as it has been possible to define those factors.

Experimental Records.

Records were kept of the nature and rate of appearance of virus disease symptoms at intervals throughout the growing season.

Counts were made of the numbers of flower buds produced on every truss up to the fifth, and these, together with the counts of the numbers of mature fruits, made possible an estimate of the effect of the particular virus studied on the setting and maturing of fruit.

Fruit picking began on May 17th and continued until the middle of September. Two or three weekly pickings were made and the number, weight and quality of the fruit from each truss were recorded, together with any special symptom pictures associated with the virus disease.

It was hoped to obtain estimates of the net assimilation rates, but it was found impracticable to estimate either dry weight or leaf area of the plants, so that indices of vegetative activity were confined to weekly counts of leaf numbers and the height of the main axis during the nine weeks between inoculation and the stopping of the shoots between the sixth and seventh flower truss.

SYMPTOMS OF DISEASE IN THE FOLIAGE.

For conciseness, the symptoms and dates at which the observations were made, have been expressed in tabular form. (Tables I-IV.) Record was kept of every plant in the experiment (48 plants per treatment). The results are perhaps remarkable for the great diversity of symptom-pictures which the presence of any one virus may induce.

Key to Abbreviations.

H No symptoms, i.e. presumed healthy.
G Light and dark green foliar mottle.
Y Yellowish-green foliar mottle.
N Necrotic spots on the youngest leaves.
S Brown stem lesions or streaks.
C Spiky-leaf or "nettlehead" symptoms of Cucumber Virus 1 (Plates 1 and 2).
D Distortion and/or blistering of the leaves.
T Thread-like leaf lamina or shoe-string symptoms.
E Enations, or leafy outgrowths, on the undersides of the leaves.
F Yellow flecking of the leaf plus general mottle.

Cucumber Virus No. 1.

Three weeks after inoculation only 4 plants out of 48 showed any recognizable symptoms of disease. As Ainsworth (1935) had pointed out that only a certain percentage of tomato plants become infected when mechanically inoculated with this virus, it was deemed advisable to repeat the inoculation using a more concentrated extract of the infectious juice. This was done on April 23rd, i.e. 25 days after the first inoculation. By mid-August not more than 10 plants showed symptoms which could be identified as due to Cucumber Virus No. 1. Identification by inspection is complicated by the fact that this virus may induce in tomato only a mottle (Ainsworth, 1935). In Table I the numbers of plants exhibiting symptoms of doubtful origin are enclosed in brackets.

TABLE I.

Symptoms Induced by Cucumber Virus No. 1.

Plants inoculated March 29th and April 23rd.

Date.	No. of plants showing symptoms thus :										
	H	G	Y	N	S	C	CG	CGN	CD	CDE	CDET
April 9th ..	48										
April 10th ..	48										
April 13th ..	48										
April 16th ..	44					4					
April 20th ..	43	(1)				4					
April 23rd ..	43	(1)				4					
April 26th ..	44	(1)				3					
April 30th ..	44	(1)				3					
May 2nd ..	36	(9)				3					
May 7th ..	32	(11)				5					
May 10th ..	13	(28)	(2)	(1)		3	1				
May 15th ..	7	(36)	(1)		(1)	2	1				
May 18th ..	4	(33)	(7)		(1)	1	1				
May 21st ..	3	(37)	(3)		(1)	1	3				
May 24th ..	3	(36)	(5)	(1)		1	2				
May 27th ..	2	(34)	(7)			1	4				
May 31st ..	0	(42)				1	4	1			
June 7th ..	0	(36)	(6)			0	2	0	1	3	
July 11th ..	0	(14)	(24)			1	7			1	1

The first sign of disease due to this virus on a crop plant was a very slight glossiness of the upper epidermis of the leaf and a slight cut-leaf effect in the young leaves, which gave the plant a spiky or nettleheaded appearance (Plate I, Fig. 1). Later, this effect sometimes became severe (Plate I, Fig. 2) and occasionally eventuated in the suppression of the lamina producing the well-known shoe-string symptoms.

Reference to Table I indicates that the nettlehead symptoms tended to disappear as the season advanced, although at later stages they reappeared in modified form in association with small enations in a few plants or in combination

with other leaf symptoms. Thus, on August 20th, a single shoot of one infected plant exhibited fern leaf, shoe-string, small enations, leaf distortion without mottling and a yellowish green mottle on successive leaves.

Tomato Mosaic Viruses and Tobacco Mosaic Virus No. 1.

Tables II, III and IV summarize the symptom records for the plants inoculated with these viruses. The incubation period of each virus was ten days and every plant inoculated became infected.

Fig. 3 indicates graphically the fluctuations in the numbers of plants inoculated with the three viruses that showed light and dark green and yellowish-green mottles for the three weeks subsequent to inoculation. The distinction between these two types of mottling is somewhat arbitrary, but an observer checking the plants daily can make the distinction with reasonable consistency. Ten to twelve days after inoculation, the relative severity of the mottling was in the order expected from earlier tests made with these three viruses on seedling plants. After this initial phase, the foliar mottle tended to become of a more or less uniform hue in all groups, although the severity, as judged by counts of light and dark green and yellowish-green mottled plants, fluctuated with changes in the environmental conditions. After the first two weeks it was not possible to differentiate the diseases caused by these three viruses merely by casual inspection of mottled leaves.

TABLE II.

Tomato Mosaic Virus (Strain A.17).

Plants inoculated March 29th.

Date.	Number of plants showing symptoms thus :						
	H	G	Y	GN	GNS	GD	GDE
April 8th		34	13		1		
April 10th		19	27		2		
April 13th		25	22		1		
April 16th		39	8		1		
April 20th		47			1		
April 23rd		47	1				
April 26th		48					
April 30th		48					
May 2nd		2				28	18
May 7th		4				33	11
May 10th		43	5				
May 15th		47	1				
May 18th		42	6				
May 21st		38	10				
May 24th		37	11				
May 27th		30	17	1			
May 31st		12	35	1			
June 7th		18	29	1			
July 11th		48					

TABLE III.

Tomato Mosaic Virus (Strain A.15).

Plants inoculated March 29th.

Date.	Number of plants showing symptoms thus :							
	H	G	Y	GN	GNS	GD	GDE	F
April 8th ..	1	44	2	1				
April 10th ..		30	16		1			
April 13th ..		32	13		2			1
April 16th ..		42	5		1			
April 20th ..		48						
April 23rd ..		48						
April 26th ..	4 ?	44						
May 2nd ..		13	2			30	3	
May 7th ..		9	1			33	5	
May 10th ..		47	1					
May 15th ..		47		1				
May 18th ..	1 ?	47						
May 21st ..		46	2					
May 24th ..		48						
May 27th ..		44	4					
May 31st ..		42	6					
June 7th ..		46	2					
July 11th ..		48						

TABLE IV.

Tobacco Virus No. 1.

Plants inoculated March 29th.

Date.	Number of plants showing symptoms thus :					
	H	G	Y	GN	GNS	YD
April 8th	2	45		1		
April 10th	1	46			1	
April 13th		32	15		1	
April 16th		39	8		1	
April 20th		47			1	
April 23rd		48				
April 26th		48				
April 30th		47		1		
May 2nd			15	1		32
May 7th		17	2			29
May 10th		13	35			
May 15th		36	12			
May 18th		29	19			
May 21st		29	19			
May 24th		27	21			
May 27th		18	30			
May 31st		14	34			
June 7th		15	33			
July 11th		48				

Streak Lesions.

In the early stages of the diseases caused by inoculation with the Tomato Mosaic Viruses, two plants in each group developed dark-brown stem-lesions (Plate II, Fig. 3), and one plant inoculated with Tobacco Virus No. 1 developed pale-brown stem lesions (Plate II, Fig. 4). From this last-named plant, inoculations were made to test plants of White Burley tobacco, *N. glutinosa*, and to tomato seedlings, and the presence of Tobacco Virus No. 1 was confirmed. The association of streaks with this virus in the tomato does not appear to have been noted previously. All five cases showing streak lesions recovered within two weeks and the plants bore fair crops of fruit.

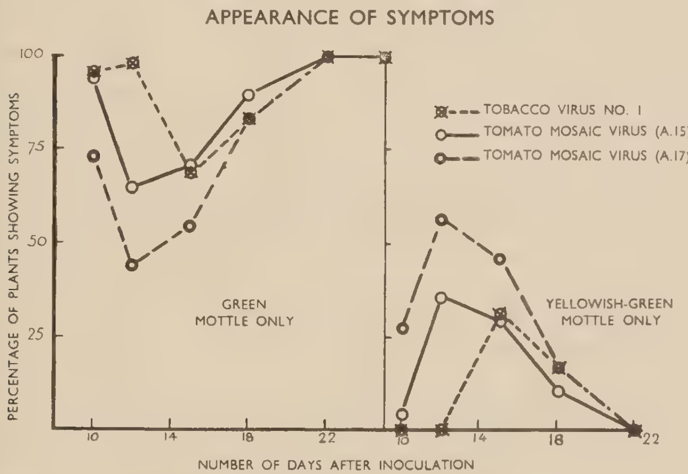


FIG. 3.

When streak lesions are present, it has frequently been noted that an environmental factor is tending to check the normal, free growth of the infected plant. A mineral deficiency may induce stem lesions, e.g. lack of potash, as Bewley (1919) indicated ; or a porous soil which has been allowed to dry out temporarily may do so, as was believed to have been the case in this experiment. Stem lesions have also been noted in tomato plants infected with the virus of tomato Aucuba Mosaic and also with the Spotted Wilt Virus. There is some evidence from commercial nurseries to show that stem lesions are associated with faulty cultural methods occurring in conjunction with a virus disease.

Enations.

A temporary phase of leaf distortion without mottling and accompanied by enations on the underside of the leaves, was noted on plants inoculated with the two Tomato Mosaic Viruses on May 1st, that is 5-6 days after the first heavy

watering had been given. Only a few leaves on each inoculated plant were affected, and later-formed leaves were mottled and of normal shape. Plate III, Figs. 5 and 6 picture two types of enation, the former being small outgrowths in the centre of the lamina and the latter large frilly outgrowths on the edges of the leaves.

The plants inoculated with Tobacco Virus No. 1 showed at this time a marked increase in the number of them that showed a yellowish-green mottle, but no enations were found on them.

In view of the fact that the Control plants showed no symptoms at the time when the infected plants were producing enations, it may be presumed that the presence of virus is directly related to the production of these outgrowths.

Records of the occurrence of enations on crop plants at this Station, show that the condition is generally confined to the month of May in the South of England and to June in Scotland. These are also the times when meteorological factors favour free growth, but watering is carefully limited until the first truss has set. The plants are usually rather hard at first, hardness being associated with a low water content and an accumulation of carbohydrates in the leaves. When a healthy plant, hardened by withholding water in a warm sunny environment, is watered freely, the interveinal leaf tissue and the thin-walled parenchymatous tissues surrounding the vascular tissue expand readily and at approximately the same rate, so that growth of the main veins and expansion of the lamina tend to proceed fairly evenly. In the leaves of infected plants there is frequently an accumulation of starch (Ainsworth and Selman, 1936) and this, together with the hardening effect induced by withholding water, will presumably lead to a thickening of the mesophyll cell walls. When water is made available to the diseased plants, the thin-walled, veinal tissues apparently extend more rapidly than the interveinal cells, and this might lead to the distortion and wrinkling of the leaf lamina which was observed in this experiment during the first week of May. Persistent inability of the cells to expand rapidly, despite adequate supplies of water, minerals and carbohydrates might then lead to the formation of outgrowths from the undersides of the leaves.

Such a mode of origin would accord with the findings of Jensen (1933), who has shown that a Mosaic infection of Nicotiana *sp.* would induce enations readily when the plants were kept well lighted and watered, but shaded plants or plants in dry soil, produced either smaller outgrowths or none at all. Thus, factors tending to limit the free, vegetative growth of an infected plant will also tend to inhibit any tendency to enation production.

Enation Mosaic has been described as a tomato virus disease by Ainsworth (1937), who considered it to be due to a distinct strain of the Tobacco Virus No. 1 (J. Johnson) type. The difficulties of the systematist are very evident, for two distinct strains of one virusmay cause the exhibition of the diagnostic features

of a third strain at various stages in the life history of the host plant. If, as seems evident, enations can be induced by many viruses at different seasons, in response to fluctuations of soil and meteorological factors, one may be witnessing phases in the generation of a new virus strain ; for, in the type described by Ainsworth, the capacity for enation production apparently persists for long periods in sub-culture.

Wilting Symptoms.

During the week following the appearance of symptoms, severe wilting of the tops occurred in the plants inoculated with the Tomato Mosaic Virus (Strain A.17), particularly in the morning when the ventilators were opened. This flagging was apparent, though to a less extent, in the plants inoculated with Strain A.15 of this virus, and in those inoculated with Tobacco Virus No. 1. It is interesting to record that severe wilting is a common symptom in plants grown on the silt soils of the Worthing area, and has been found to be associated with acute attacks of virus disease. This effect has been reported with Mosaic infection of tobacco (Allard 1914) and of cucumber and pumpkin (Doolittle, 1920), Wilting was not observed after this initial phase, the house being kept slightly warmer and more humid thereafter.

Effect of Air Temperature on Leaf Mottling.

In contrast to the severe symptoms described above, several plants inoculated with Strain A.15 appeared to be quite free from infection at various times in the season. Complete symptom masking of badly Mosaic-infected tomato plants was noted by Freiburg (1917) when the average temperature of the air was 85° F. It has since been shown by Tompkins (1926) that the masking of potato Mosaic symptoms in a greenhouse is directly influenced by air temperature and by the daily duration of exposure to that temperature. A correlation was therefore sought between the changes observed in the intensity of the foliar mottle and the air temperature. The ten-day period immediately preceding the symptom counts, was chosen arbitrarily, in view of the fact that the incubation period of the viruses was of this duration, and it was assumed that subsequent changes in the plant symptoms might require a similar period.

Very high partial correlation coefficients (time eliminated) were found for the Tomato Mosaic Viruses and Tobacco Virus No. 1 between the percentage of plants showing a light and dark green leaf mottle only, and the mean daily number of hours for which the air temperature exceeded 70° F. Tables V and VI show the relevant data and the correlations calculated from them.

Similar values were obtained for temperatures above 75°, 80° and 85° F., but no such high correlation was found for temperatures above 65° F.

Under glasshouse conditions there is frequently a high correlation between light intensity and air temperature. No measurements were made of light intensity, so that the influence of this important factor cannot be dissociated from the temperature effect in this experiment. Tompkins concluded that air temperature was the only factor affecting the masking of potato Mosaic symptoms, and it may not be unreasonable to suppose that temperature will play an important part in determining the intensity of virus disease symptoms in the tomato. It should be pointed out that Tompkins was concerned only with investigating the

TABLE V.

Air Temperature and Mottling.

Mean daylight hrs. over 70° F.	Date.	% Plants showing green mottle only.		
		T.M.(A.17).	T.M. (A.15).	TbV.1.
9·5	April 8th	71	92	98
8·7	April 10th	40	62	98
8·4	April 13th	52	67	67
9·5	April 16th	81	88	81
10·3	April 20th	98	100	98
10·6	April 23rd	98	100	100
9·9	April 26th	100	100	100

TABLE VI.

Partial Correlation Coefficients.

Virus.	Mean no. of daylight hrs. over 70° F. and % plants showing green mottle only.		
		"t"	"p"
Tomato Mosaic (A.17) ..	0·963	4·195	0·02—0·01
Tomato Mosaic (A.15) ..	0·993	18·97	less than 0·01
Tobacco Virus No. 1 ..	0·995	22·25	,, ,, ,,

effect of environmental factors singly (with the exception of soil moisture and soil temperature, which were investigated at different levels simultaneously), and his nutrition studies were very limited.

The variations in leaf mottling displayed later in the season, may have been induced partly by fluctuations in the internal nitrogen level of the plants, brought about by the heavy demands made by the fruit on the available supplies. Dressings of nitrogenous fertilizers certainly appeared to reduce the severity of the mottling in June and July.

FLOWERING, FRUITING AND VEGETATIVE GROWTH.

Statistical Analysis of Data.

In the present circumstances it is not possible to publish the primary data in full, but in the three Tables in the Appendix are included the treatment and truss-treatment means of the recorded data. One example of the method of statistical analysis is given below, and in subsequent sections only the " z " values have been recorded, significant values being printed in heavy type. In the accompanying figures the magnitude of a significant difference is indicated by the vertical lines to the right of the graphs. It should be pointed out that where five trusses have been measured separately, Mean Square Deviations (*a*) would represent 1/5 of the variance of a single plot, the unit in the analysis being the truss and not the whole plant, which consisted of five trusses.

Production of Flower Buds.

Counts were made of the number of flower buds on each truss as they appeared. In examining the effect of viruses, the number of buds in the first truss was not included in the analysis, as in all cases the buds of this truss were actually differentiated before the plants were inoculated.

Analysis of Variance.

Number of Flower Buds. (Trusses 2-5 inclusive).

	D.F.	Mean Square	" z "	5% pt.
Between plots :				
Treatments	4	239·8	**0·5335**	0·5265
Blocks	5	51·2		
Deviations (*a*)	20	82·5		
Within plots :				
Trusses	3	106·0	**0·6067**	0·4787
Interaction (Trusses × Treatment)	12	32·0	0·0078	
Deviations (*b*)	75	31·5		
Total	119			

The treatment and truss-treatment means are shown graphically in Fig. 4. The importance of truss position is evident in this and subsequent analyses of variance, but the data will not be expanded further as the relationships involved do not fall immediately within the scope of this paper.

The Control plants produced more flower buds than the early inoculated plants, but no significant differences were found between plants inoculated with Tobacco Virus No. 1 and those inoculated with the two Tomato Mosaic Viruses. The greatest difference between the Control and the treated plants occurred in the fourth truss. This exceeds three times the standard error and may be regarded as significant, despite the non-significant interaction, since the experiment was, from the first, designed to test such comparisons.

Number of Fruits.

The number of mature fruits from each truss was counted at each picking. Analysis of the data revealed the following results :—

	" z "	0·1% point.
Treatments ..	1·2401	0·9798
Trusses	1·2871	0·7648
Interaction ..	0·8352	0·5044

The mean values are shown graphically in Fig. 5. The number of fruits was reduced by Tobacco Virus No. 1 and by the two Tomato Mosaic Viruses

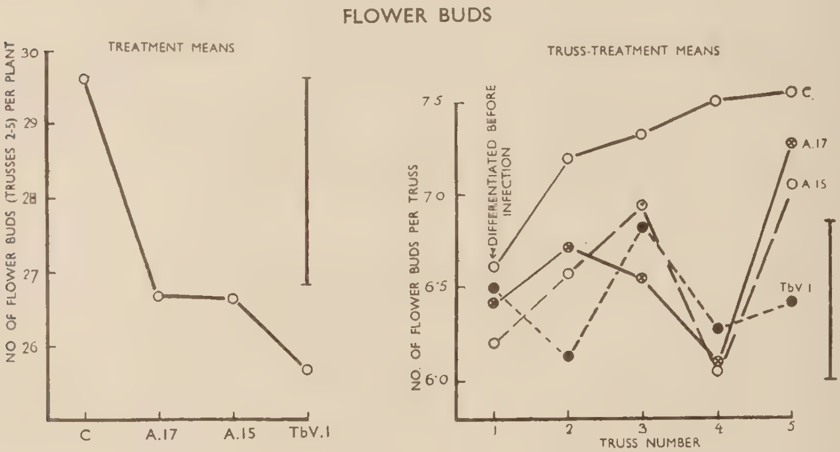


FIG. 4.

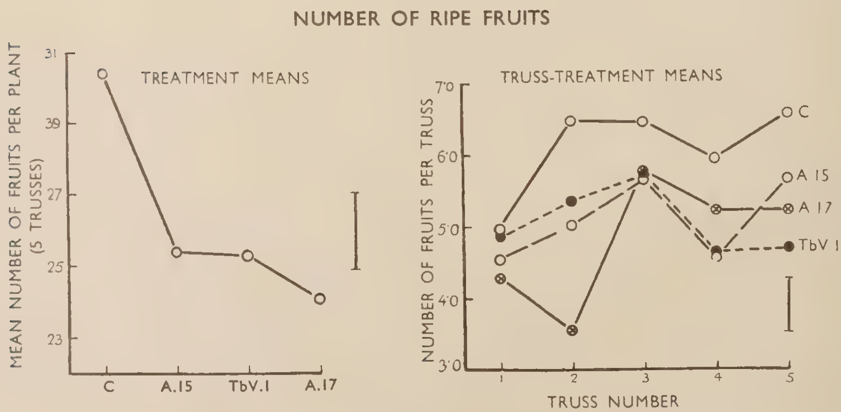


FIG. 5.

relative to the Controls. The number of fruits was least in the Tomato Mosaic Virus (Strain A.17), which was accounted for in large measure by the severe reduction occurring in the second truss.

Fruit Set.

The ratio of the number of mature fruits to the number of flower buds provides a measure of the "goodness of set", although no data are available which might indicate the precise stage of pollination or fruit development at which the viruses are likely to be detrimental. The "z" values were as follows :

	"z"	0·1% point.
Treatments ..	1·0167	0·9798
Trusses	1·0799	0·7648
Interaction ..	1·0422	0·5044

It may be noted that the use of the function θ (where

$$\sin^2 \theta = \frac{\text{Percentage flower buds producing fruit}}{100})$$

in the analysis of variance, did not affect the levels of "z" appreciably.

FLOWER BUDS PRODUCING FRUIT

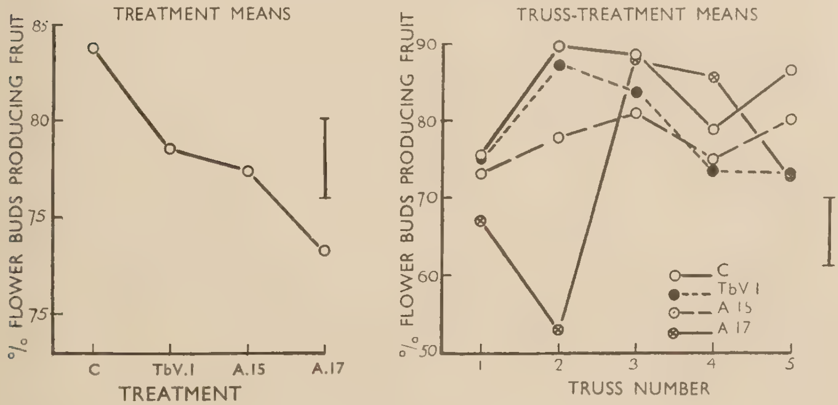


FIG. 6.

Reference to Fig. 6 will indicate the serious effect of the Tomato Mosaic Virus (Strain A.17) in reducing the percentage of flower buds producing good fruit. This effect was most marked in the second truss. The treatment means for the whole plant show that this virus was also effective in reducing the percentage

of fruit produced to a significantly lower value than that caused by Tobacco Virus No. 1 and the Tomato Mosaic Virus (Strain A.15), respectively.

Average Fruit Weight.

From the parallel results recorded for total yield and total number of fruits, it was anticipated that the effect of treatments upon average fruit weight would not be large. The "z" tests were as follows :—

	"z"	
Treatments	0·3827	(0·5265=5% point)
Trusses	**2·0054**	0·7648=0·1% point
Interaction	0·1964	(0·2804=5% point)

Thus the average fruit weight was not seriously affected by the treatments in this experiment.

Yield of Ripe Fruit.

Under this heading were included fruits of all grades both blemished and sound. Weighing was carried out on a simple balance to the nearest ¼ ounce. For comparative purposes the mean yields have been converted to tons per acre. (Appendix Table I, and Fig. 7), and it is thus evident that the yield of the Control series (25·8 tons per acre from 5 trusses) was comparable with the yields of the average successful commercial nursery which normally produces 50-60 tons per acre from 10-15 trusses.

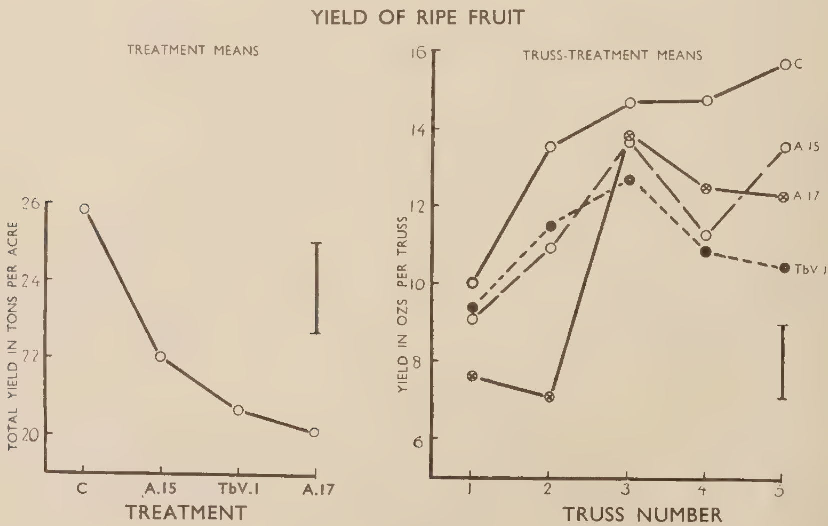


Fig. 7.

Fig. 7 illustrates graphically the effects of early virus infection on yield. The "z" tests were as follows :—

	"z"	0·1% point.
Treatments ..	**1·0717**	0·9798
Trusses	**1·7888**	0·7648
Interaction ..	**0·7555**	0·5044

The most important yield reduction occurred with the Tomato Mosaic Virus (Strain A.17) in the first two trusses. In later trusses there was an increase in the percentage of buds setting fruit, which is manifest in a "recovery" in yield of ripe fruit.

Table VII summarizes the mean yield reductions relative to the Controls of the three main treatments, together with the reduction in number of fruits and flower buds for the five truss totals :—

TABLE VII.

Percentage Reduction Relative to Controls.

	Yield.	No. of fruits.	No. of flower buds.
Tomato Mosaic Virus (Strain A.17) ..	22·3	20·9	8·7
Tobacco Virus No. 1	20·1	17·0	13·4
Tomato Mosaic Virus (Strain A.15) ..	14·7	16·5	9·5
Mean	19·03	18·13	10·50

The mean values for the three viruses given in Table VII suggest that at least three factors were operative in bringing about a reduction in yield :

(1) Failure of flower buds to differentiate.

(2) Failure of flower buds to set and mature fruit.

(3) A reduction in average fruit weight, the concomitant of a lowered growth rate and a smaller plant.

The relative importance of these factors was found to vary amongst the viruses investigated ; thus, failure of the fruit to set was more serious with the Tomato Mosaic Virus (A.17) than with Tobacco Virus No. 1., whereas with the latter the failure of the flower buds to differentiate apparently contributed markedly to the crop reduction. Average fruit weight, though not significantly affected by treatments, actually showed a slight non-significant increase with the Tomato Mosaic Virus (A.15).

Statistically, the failure of the flower buds to mature fruits is highly significant, in contrast with the other two effects.

Blotchy Fruit.

Ripe fruits showing pits or irregular pigment development (excluding "greenback") were weighed separately, and the weight of blotchy fruit was recorded as a percentage of the total yield. The faint mistiness of the pigment, which is exhibited by almost all virus-infected fruits, was ignored in this classification, since it is disregarded by nurserymen in grading fruit for market.

A small percentage of blotchy fruit was recorded in the Control series, a result of late infection. Analysis of the data showed that treatments and the truss-treatment interaction just failed to reach the conventional level of significance. Relative to virus-free plants, it is almost certain that all the early infected plants would have borne significantly more blotchy fruit under the conditions of this experiment.

	"z"	
Treatments	0·4350	(0·5265=5% point)
Trusses	**0·8402**	0·7648=0·1% point
Interaction ..	0·2123	(0·2804=5% point)

The importance of the position of the truss in determining the amount of blotchy fruit, may be related to temporary mineral deficiencies in the plant tissues at certain stages of growth.

The small differences found between the inoculated and the Control plants for the percentage of blotchy fruit, suggest that time of infection is not of paramount importance in determining the amount of blotchy fruit. The most severe fruit pitting and mottling was actually found on a plant of the Control series which did not show signs of infection until the fifth truss was in bloom. The reason for this severe attack was not clear, however, since only one plant out of 48 showed these symptoms.

From the practical point of view it would appear that the losses to the grower from the reduction in total yield would, under conditions similar to those of the present experiment, far exceed those due to the production of blemished fruit.

The statement that Tobacco Virus No. 1 does not cause marking of the fruit (Ainsworth, 1933) is apparently not always true, although the degree of mottling is usually much milder than that due to the more virulent viruses. Earlier descriptive work has frequently been based on the reactions of smaller plants grown in pots, and it may be noted that only a very small amount of blotchy fruit was produced on the first truss of the plants inoculated with Tobacco Virus No. 1 (0·3%).

Types of Fruit Markings.

In addition to faint blotchiness of the skin colour of the ripe fruit, the following more severe symptoms were also noted :—

(1) *Cucumber Virus No. 1.*

A few plants inoculated with this virus, the presence of which had been confirmed by transference to cucumber plants, produced fruits with a distinctive green and red mosaic. The coloured areas were sharply demarcated *without* gradation of colour, and no pits were present.

Several plants bore fruits showing irregular, glazed whitish areas. Neither of these fruit symptoms appeared on any of the Mosaic infected plants.

(2) *Tomato Mosaic Viruses and Tobacco Virus No. 1.*

The familiar yellowish or orange mottle was found on some of the fruits from plants inoculated with these three viruses. No distinctive patterns could be

TABLE VIII.

Numbers of Pitted Fruits.

Block.	Control (late infected).	T.M. (A.17).	T.M. (A.15).	TbV.1.
A	0	3	1 (slight)	0
B	1	1	0	1 (slight)
C	0	0	0	0
D	1	0	0	0
E	14	0	0	0
F	0	0	3	0

discerned which might be used to identify any of these viruses, but pitted fruits were found on a few plants.

Fruit pitting has been attributed to several virus or bacterial agents as Ainsworth (1933) has pointed out; of these the virus of Tomato Mosaic (Bewley) is probably the most widespread in this country. The occurrence of this symptom was found to be irregular and bore no simple relation either to the position of the plant in the house or to the association with any one of the viruses here investigated. Table VIII shows the numbers of pitted fruits per plot (8 plants).

Greenback.

A very small percentage of fruits was recorded in which the hard, green, calyx-end ripened out slowly. No factors within the scope of the experiment could be shown to be related to the incidence of this trouble.

Leaf Production.

Leaf counts were made on marked plants selected at random, one per plot, at the beginning of the experiment. These counts were carried out over the nine-week period subsequent to inoculation of the plants. During this period all the plants of the Control series showed no symptoms and were presumed to be healthy. Leaves on the main axis 0·75 inches in length and over, were counted. "z" tests on the weekly rates of leaf production were :—

	"z"	
Treatments ..	0·4105	(0·5265=5% point)
Sampling times ..	**1·5152**	0·6599=0·1 point
Interaction ..	**0·2799**	0·2085=5% point

Thus, although the total number of leaves produced in this period was slightly reduced by virus infection, the reduction did not quite reach the 5% level of significance for "z". The significant interaction of treatment with sampling time is reflected in Fig. 8 where a fall in weekly leaf production rate is seen to occur with the plants inoculated with the Tomato Mosaic Virus (A.17) during the week following inoculation, i.e. at the time of appearance of symptoms. Smaller non-significant decreases were also noted at this time for plants inoculated with Tobacco Virus No. 1.

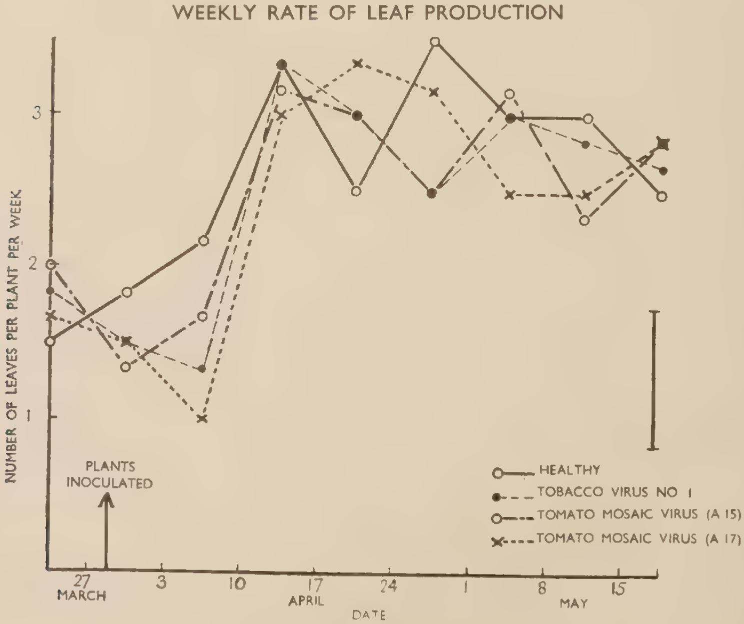


Fig. 8.

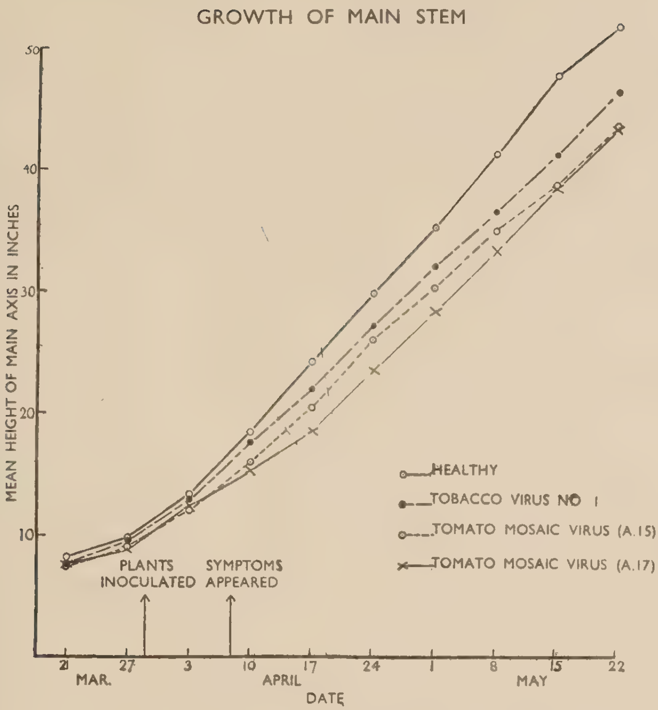


FIG. 9.

Watson and Baptiste (1938) have discussed the significance of the rate of leaf production as here defined, and consider that over a prolonged period it may be regarded as a measure of meristematic activity. Hence it may be suggested that apart from an initial check, meristematic activity was not affected by the presence of virus under the conditions of this experiment.

Height of Main Axis.

The marked plants used for the leaf counts were also measured at weekly intervals and for the same period, to determine the growth rate of the main stem. All side shoots were removed at ten day intervals, so that growth was confined to the single axis. Measurements were discontinued when the growing tops were in contact with the roof of the house. The mean growth curves (6 plants per treatment) are given in Fig. 9. Statistical analysis of the weekly height increments showed the following " z " values :—

	"z"	
Treatments ..	0·6863	0·5265=5% point.
Sampling times ..	1·0957	0·6599=0·1% point.
Interaction ..	0·4059	0·3786=0·1% point.

As with the rate of leaf production, the greatest reduction in weekly growth rate occurred with plants inoculated with the Tomato Mosaic Virus (Strain A.17) during the week in which symptoms appeared.

The final stem heights (May 22nd) showed that virus infection had checked growth, although to a less degree with the Tobacco Virus No. 1 than with the two Tomato Mosaic viruses. Fitting linear regression curves to the data indicated the same general conclusion. The linear regression coefficients of height on sampling time are given in the Appendix Table III, together with the mean weekly height increments and rates of leaf production.

Discussion of Results.

It has long been recognized that the yield of tomato plants may be reduced by virus infection. Heuberger and Moyer (1931), who reviewed the earlier work, showed that the time of infection was of importance in determining the magnitude of losses occurring in field-grown tomatoes. Their earliest infected plants suffered crop losses of 56% relative to the Controls.

The several causes to which crop reduction may be attributed, have been pointed out by many workers. Thus, Westerdijk (1910) noted the incidence of blossom drop in plants affected with Tomato Mosaic before fertilization had taken place. In Maryland, Norton (1914) reported that healthy tomato plants set 33% more fruits than virus diseased ones, although the actual weight of fruit was scarcely affected by Tomato Mosaic. On cucumber, Doolittle (1920) noted the greatly reduced numbers of pistillate flowers borne by virus-infected plants. Dickson (1922) recorded up to 30% flower fall on tomato and raspberry affected with Mosaic in the field, and similar effects with potato, sweet pea and bean suffering from virus diseases. A few data are given by Heuberger and Moyer (1931) which suggest that early infection resulted in fewer fruits set in the tomato. With Bean Mosaic, Harrison (1935) showed that fewer blooms per plant were produced, although per unit of dry matter there was actually a greater number of blooms on the affected plants than on the healthy ones. Working with Potato Mosaic in the field, Stone (1936) concluded that there was a reduction in the photosynthetic efficiency of the plant, with a reduction in the growth rate of the stem.

Thus, the conclusions reached in the present experiment concerning the effect of certain viruses on tomato flower bud differentiation, fruit set, vegetative growth, etc., are in general accord with the findings of earlier workers on a number of virus diseases. Quantitative data do not appear to have been presented hitherto for simultaneous observations on flowering, fruiting and vegetative growth of the plant.

The fact that meristematic activity, as measured by the rate of appearance of leaves, is not seriously affected by virus infection, may be of considerable

importance, in view of the fact that viruses have been shown to be proteins, and meristems are active centres of protein metabolism. The initial check to leaf production at the time of appearance of symptoms is rapidly overcome, thus suggesting that after a preliminary readjustment, the meristems are capable of elaborating the abnormal virus proteins as readily as normal proteins.

Chemical analysis and the study of the vegetative and reproductive responses of the plant have shown that virus infection may induce profound changes in plant metabolism. In the present experiment, data on some of the macro-responses of the plant, afford an indication of the relative importance of some of the processes affected by virus attack in relation to the final yield. These data give little clue as to the sequence or relative importance of the internal changes within the plant. For example, failure of the flower buds to differentiate, might, on physiological grounds, be interpreted as the result of a shortage of available nitrogen, as that of a deficit of water within the plant or as that of a combination of both these factors. In view of the fact that nitrogen metabolism and the water relations of the plant are known to be seriously affected by virus, it might be of considerable practical value to be able to assess the relative importance of these factors in determining the magnitude of virus-induced reductions in the numbers of flower buds. Further work along these lines is now in progress.

In connection with the application of cultural control methods as recently outlined by the author (1941), the results reported here indicate the importance of the initial phase of infection at the time of appearance of symptoms. It is at this time that the most serious interference with normal metabolism apparently occurs, and it is reflected in the most severe reductions in growth rate, meristematic activity and in the fruit set of the flowers in bloom at that time. Also, this was the only time during which stem lesions were produced in the infected plants. If the deleterious effects of virus can be reduced at all by cultural methods—and practical experience of growers suggests that they can be so reduced—then the first appearance of symptoms should be most carefully watched for, and cultural efforts then directed towards countering any abnormal or undesirable growth which infection is known to induce.

SUMMARY.

(1) An experiment is described in which the effect of Tobacco Virus No. 1 (J. Johnson) and of two strains (A.15 and A.17) of Tomato Mosaic Viruses (Bewley) on the growth, flowering and fruiting of a tomato crop under glass, have been investigated. The plants were artificially inoculated when the first truss was in bloom and the reactions of these plants were compared with Control plants which showed symptoms of accidental infection, but not until the fifth truss was in bloom.

(2) The diversity of the symptom-pictures which may be induced by the presence of one or other of these viruses (and also of Cucumber Virus No. 1, which was successfully inoculated into a few plants) at different times in the season and in the same plant is pointed out.

(3) Enations were found in association with Cucumber Virus No. 1 and with the two strains of a Tomato Mosaic Virus, but not with Tobacco Virus No. 1.

(4) The origin of enations is discussed. There is evidence that these can be induced in infected plants which are allowed to develop freely after subjection to hardening conditions.

(5) Light-brown stem streaks appeared on one plant inoculated with Tobacco Virus No. 1.

(6) Severe wilting of the plants inoculated with one strain of Tomato Mosaic virus was noted at the time of appearance of symptoms.

(7) High partial correlation coefficients were found to exist between the mean number of daylight hours during which the plants were exposed to temperatures of 70° F. or over and the percentage of plants showing a mild, light and dark green foliar mottle only. This correlation was shown for the two Tomato Mosaic Viruses and for Tobacco Virus No. 1.

(8) Control plants produced significantly more flower buds on trusses 2-5 than did early-infected plants, the greatest difference occurring in the fourth truss.

(9) A significant reduction in the number of fruits picked was occasioned by early infection. The most serious reduction occurred with the second truss of the plants inoculated with a strain of Tomato Mosaic Virus.

(10) The percentage of flower buds producing fruits was lowered by early infection, in all cases. The plants inoculated with the virus of Tomato Mosaic (Strain A.17) set a significantly smaller percentage of buds than those infected with Strain A.15 of this virus or with Tobacco Virus No. 1.

(11) The total yield of ripe fruit from five trusses was reduced by all treatments relative to the Controls, thus :—

Tomato Mosaic Virus (A.17) induced a 22·3% reduction in yield.
Tobacco Virus No. 1 induced a 20·1% reduction in yield.
Tomato Mosaic Virus (A.15) induced a 14·7% reduction in yield.

(12) Yield reduction appears to be related to the following causes :—

(1) Failure of flower buds to differentiate.

(2) Failure of flower buds to set and mature fruit.

(3) A slight reduction in average fruit weight.

(13) Early infection induced small, although non-significant increases in the percentage of blotchy fruit produced. Tobacco Virus No. 1 infection was associated with small amounts of blotchy ripening.

(14) A small, non-significant reduction in the weekly rate of leaf production was recorded with infected plants relative to the Controls during the nine weeks following inoculation. A marked, though temporary, check was noted at the time of appearance of symptoms.

(15) Infection significantly reduced the weekly height increment of the main stem during the first nine weeks of the experiment relative to the Controls.

(16) The time of appearance of symptoms is considered to be the most critical stage in the metabolism of an infected plant. The importance of this stage in devising cultural control methods is pointed out.

ACKNOWLEDGMENT.

The author wishes to record his sincere thanks to Dr. W. F. Bewley for much helpful advice throughout the course of this work and for granting the extended facilities which made the experiment possible.

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APPENDIX.

TABLE I.

Summary of Treatment Means.

	Control.	Tomato Mosaic Virus (A.17).	Tomato Mosaic Virus (A.15).	Tobacco Virus No. 1.	Control X.	Mean. S.E.
No. of Flower buds per plant (trusses 2-5)	29·61	26·67	26·63	25·67	28·40	27·39 ±0·927
% Flower buds producing fruit (5 trusses)	83·82	73·32	77·41	78·53	77·76	78·17 ±1.356
No. of fruits per plant (5 trusses) ..	30·40	24·04	25·40	25·25	27·08	26·44 ±0·714
Average fruit weight (ozs.)	2·252	2.183	2·306	2·174	2·309	2·245 ±·0453
Total yield of fruit: Oz. per plant (5 trusses) ..	68·75	53·44	58·65	54·96	61·88	59·53 ±2·092
Tons per acre (5 trusses) ..	25·83	20·07	22·03	20·64	23·23	22·36 ±0·786
% severe blotchy fruit by weight (5 trusses)	5·41	10·63	6·73	5·58	7·44	7·16 ±1·367

TABLE II.

Summary of Truss Means.

No. of Flower Buds per Truss.

Truss No.:	1	2	3	4	5
Control	6·62	7·20	7·33	7·50	7·56
Tomato Mosaic Virus (A.17)	6·42	6·72	6·56	6·10	7·27
Tomato Mosaic Virus (A.15)	6·21	6·58	6·95	6·04	7·04
Tobacco Virus No. 1	6·50	6·14	6·83	6·27	6·42
Control X	6·60	7·18	7·37	6·83	6·99

Mean = 6·84 S.E. = ±0·286 (Trusses 2-5 inclusive).

% Flower Buds Setting and Maturing fruit.

Truss No.:	1	2	3	4	5
Control	75·35	89·82	88·50	78·92	86·50
Tomato Mosaic Virus (A.17)	67·03	52·98	88·05	85·67	72·88
Tomato Mosaic Virus (A.15)	73·22	77·80	80·97	74·95	80·13
Tobacco Virus No. 1	75·02	87·23	83·75	73·50	73·13
Control X	76·33	88·35	77·68	78·60	67·85

Mean = 78·17 S.E. = ±2·938

Number of Fruits per Truss.

Truss No.:	1	2	3	4	5
Control	4·98	6·47	6·45	5·94	6·56
Tomato Mosaic Virus (A.17)	4·29	3·54	5·77	5·22	5·20
Tomato Mosaic Virus (A.15)	4·54	5·02	5·65	4·54	5·64
Tobacco Virus No. 1	4·87	5·35	5·71	4·62	4·69
Control X	5·02	6·34	5·73	5·33	4·67

Mean = 5·29 S.E. = ±0·251

Total Yield of Fruit. Oz. per plant.

Truss No.	1	2	3	4	5
Control	10·02	13·56	14·69	14·77	15·71
Tomato Mosaic Virus (A.17)	7·63	7·11	13·86	12·52	12·33
Tomato Mosaic Virus (A.15)	9·06	10·96	13·67	11·31	13·61
Tobacco Virus No. 1	9·40	11·50	12·73	10·88	10·46
Control X	10·13	13·38	13·31	13·19	11·86

Mean = 11·91 S.E. = ±0·631

Weight of Blotchy Fruit. Oz. per plant.

Truss No.	1	2	3	4	5
Control	0·42	0·67	0·43	1·20	1·12
Tomato Mosaic Virus (A.17)	0·79	0·65	1·53	1·81	0·94
Tomato Mosaic Virus (A.15)	0·42	0·37	0·75	1·28	1·14
Tobacco Virus No. 1	0·03	0·36	1·27	0·70	0·80
Control X	0·26	1·07	0·76	1·15	1·56

Mean = 0·86

TABLE III.

Leaf Production. Leaves per plant per week.

Week ending	April 2nd	April 9th	April 16th	April 23rd	April 30th	May 7th	May 14th	May 21st	Total No. Leaves per plant May 22nd
Control	1·84	2·17	3·33	2·50	3·50	3·00	3·00	2·50	34·5
T.M. (A.17)	1·50	1·00	3·00	3·33	3·17	2·50	2·50	2·83	31·3
T.M. (A.15)	1·33	1·67	3·17	3·00	2·50	3·17	2·34	2·84	32·2
Tobacco Virus No. 1 ..	1·50	1·33	3·33	3·00	2·50	3·00	2·83	2·67	32·3
Control X.	1·33	2·33	2·66	3·84	2·50	2·66	1·83	2·34	31·8

Mean = 2·533 S.E. = ±0·303

Height Increments of Main Stem. Inches per plant per week.

Week ending :	April 2nd	April 9th	April 16th	April 23rd	April 30th	May 7th	May 14th	May 21st	Mean height on May 22nd
Control	4·30	5·08	5·91	5·68	5·25	6·24	6·33	4·08	51·8
T.M. (A.17)	3·33	2·92	3·17	5·25	4·67	5·00	5·17	5·00	43·6
T.M. (A.15)	3·00	4·00	4·41	5·66	4·25	4·67	3·83	4·84	43·7
Tobacco Virus No. 1 ..	3·33	4·67	4·41	5·16	4·91	4·50	4·67	5·25	46·5
Control X	3·75	4·75	5·08	6·58	4·75	4·91	3·25	3·17	46·4

Mean = 4·61 S.E. = ±0·415

Linear Regression Coefficient (b) *of Height* (y) *on Sampling Time* (x).
where $y - \bar{y} = b\,(x - \bar{x})$.

	Healthy.	T.M. (A.17)	T.M. (A.15).	Tobacco Virus.	Control X.	Mean S.E.
b	5·49	4·39	4·45	4·69	4·78	4·76 ± 0·229
$\bar{y}$	30·18	24·79	25·70	27·30	29·07	

(*Received* 9/4/41.)

THE INHERITANCE OF SUSCEPTIBILITY TO SULPHUR DAMAGE IN FAMILIES OF SEEDLING APPLES

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Compounds containing sulphur are extensively used as fungicides on apple trees, particularly for the control of Scab. That most extensively employed is a concentrated solution prepared from lime, sulphur and water, which is diluted with water before use. The degree of dilution is varied somewhat according to the season.

While most varieties of apple show no damage from applications of lime sulphur at the low concentrations necessary for the control of Scab, there are some which suffer damage to a greater or less extent. These are usually referred to as sulphur shy varieties.

Certain varieties, of which Stirling Castle and Lane's Prince Albert are the most extensively grown, are extremely susceptible to sulphur damage and severe defoliation results from applications of lime sulphur even at very low concentrations. Even if the leaves do not actually fall from the tree they frequently assume a bleached, pale green appearance, with varying degrees of marginal scorching. Cox's Orange Pippin and Beauty of Bath are the best known of a group of varieties in which the damage shows a tendency to fluctuate from one season to another and is never extremely severe. Notes on the susceptibility of most of the varieties used as parents in crosses discussed in this paper are given in Appendix A.

With varieties that are subject to severe sulphur injury it is usual to replace lime sulphur by a copper containing fungicide, such as Bordeaux Mixture, where control of Scab is necessary.

Plots on which a large number of seedling apples are growing at East Malling have received routine applications of sulphur-containing sprays each spring for a number of years. The seedlings, grown on rootstock No. IX as cordons, are of very diverse parentage. They were raised with the primary object of producing new varieties of apples of value in commercial fruit growing, although information on the genetics of the apple is also being sought.

It was early remarked that these seedling families differed strikingly in their reaction to the sulphur sprays employed. While the families of many of the crosses appeared almost completely unaffected, in others a comparatively large proportion of the seedlings became defoliated to a greater or less extent.

Families from crosses involving Stirling Castle were by far the most severely affected.

Records of the defoliation among the seedlings, taken during the summer of 1940, are summarized in Table I. Fuller details of the precise parentage of the families studied and the actual numbers of seedlings affected in each will be found in Appendix B.

TABLE I.

Relative numbers of susceptible seedlings in the principal families.

	No. of families.	No. of seedlings.	% defoliated.
Crosses involving Stirling Castle :	9	352	21
Crosses not involving Stirling Castle :			
White Transparent	3	89	7
Rote Sommer Apfel	5	192	6
Cox's Orange Pippin	10	196	5
Yellow Ingestrie	3	201	3
Devonshire Quarrenden ..	9	642	2
Laxton's Superb	2	65	2
Brownlee's Russet	4	77	1
Mc'Intosh Red	5	107	1
Golden Delicious	5	120	0

Apart from the much greater prevalence of sulphur shyness among seedlings from crosses involving Stirling Castle as one parent, there were significant differences in this respect between certain other groups of families. Families having as parents White Transparent, Rote Sommer Apfel and Cox's Orange Pippin appeared to have about the same proportion of sulphur shy seedlings. In families involving Yellow Ingestrie, Devonshire Quarrenden, Laxton's Superb, Brownlee's Russet and Mc'Intosh Red the proportion of seedlings defoliated was considerably less. None of the seedlings from crosses with Golden Delicious showed any signs of susceptibility to sulphur damage. Statistically, the odds against the much greater susceptibility of the Stirling Castle seedlings being due to chance are very great indeed.* There are odds of 100 : 1 against the difference between the first three and the last six of the remaining groups of families in Table I being due to chance.

Considerable differences in the relative number of sulphur shy seedlings existed among the families in which Stirling Castle was the female or seed parent. The data are shown in Table II.

* Through the kindness of Mr. T. N. Hoblyn the writer is able to add the following note on the method employed in the statistical analysis of the data in this paper. "The method of statistical analysis used to test the significance of these differences was a test of goodness of fit. In the test the proportion defoliated and not defoliated observed in each set of crosses was compared with those expected on the assumption that all behaved alike, using the X^2 test to assess the significance of any deviation from expectation."

Although the number of seedlings is not generally large, there are some interesting and significant differences. For instance, the cross between Stirling Castle and Lady Carrington gave an unusually large proportion of sulphur shy seedlings, while among the very few seedlings obtained from the cross with Rote Sommer Apfel no seedlings were defoliated by sulphur spray. In families from Stirling Castle crossed with Yellow Ingestrie and with Golden Russet, about one-third of the seedlings were sulphur shy, but the proportion was considerably less when Brownlee's Russet was the pollen parent. This is closely paralleled in the crosses in which Stirling Castle was not a parent, shown in Table I. In that case a somewhat larger proportion of seedlings were defoliated in crosses with Yellow Ingestrie than with Brownlee's Russet.

TABLE II.

Proportion of sulphur shy seedlings from families in which Stirling Castle was the seed parent.

Pollen Parent.	No. of seedlings.	% defoliated.
Lady Carrington	11	73
Yellow Ingestrie	8	38
Golden Russet	18	33
Brownlee's Russet	69	12
Rote Sommer Apfel.. ..	6	0

Among the crosses in which Stirling Castle was the male or pollen parent the differences in the proportion of sulphur shy seedlings were not quite so striking. They are shown in Table III.

TABLE III.

Proportion of sulphur shy seedlings from families in which Stirling Castle was the pollen parent.

Seed Parents.	No. of seedlings.	% defoliated.
Cox's Orange Pippin ..	5	40
Devonshire Quarrenden ..	154	21
Yellow Ingestrie	52	17
Brownlee's Russet	29	14

The differences between the proportions of sulphur shy seedlings in these four families are not significant. Of the two families which are the reciprocals of families in Table II, Yellow Ingestrie × Stirling Castle had considerably fewer defoliated seedlings when Yellow Ingestrie was the seed parent than when it was the pollen parent. But in the crosses with Brownlee's Russet and

Stirling Castle there was little difference between reciprocals. As might have been expected, the cross with the slightly sulphur shy Cox's Orange Pippin gave a relatively large proportion of sulphur shy seedlings.

Turning to the families of which Stirling Castle was not a parent, among those containing Cox's Orange Pippin, although the families were often small and there was considerable variation, the proportion of sulphur shy seedlings was surprisingly low on the whole, as may be seen from Table IV.

TABLE IV.

Proportion of sulphur shy seedlings from families of which Cox's Orange Pippin was a parent.

Parents.	No. of seedlings.	% defoliated.
Blenheim Orange ♂ ..	4	25
Winter Sunshine ♀ ..	35	11
Rote Sommer Apfel ♂ ..	39	8
Bascombe's Mystery ♀ ..	21	5
Laxton's Superb ♀ ..	57	2
Ellison's Orange ♂ ..	5	0
D'Arcy Spice ♀	5	0
Golden Delicious ♀	14	0
Rome Beauty ♀	4	0
St. Everard ♀	12	0

Of the ten families shown in the Table, that from the crosses between Cox's Orange and Blenheim Orange had considerably the largest proportion of sulphur shy seedlings. Of the remaining families the most interesting are those from crosses between Cox's Orange, Laxton's Superb, Ellison's Orange and St. Everard. The three latter varieties are all selections from families of which Cox's Orange was one of the parents. They have never been noted as particularly sensitive to sulphur. It is noteworthy that in two of these families none of the seedlings was sulphur shy, while in the third the proportion was rather less than two per hundred.

There was no significant difference between the percentages of sulphur shy seedlings in the three families of which White Transparent was one parent. The largest proportion, about 17 per cent., occurred in a cross with Rote Sommer Apfel.

The five families of which Rote Sommer Apfel was one parent showed considerable variation, and as at least one difference is statistically significant the data are worth considering in greater detail. They are shown in Table V.

Of these six families, that from the cross between St. Cecelia and Rote Sommer Apfel contained almost twice as large a percentage of sulphur shy seedlings as any of the other families. This difference is statistically very

significant, the odds against its being due to chance being more than 100 to 1. St. Cecelia itself is a notoriously sulphur shy variety. It is interesting to notice that the families from crosses with St. Cecelia and St. Everard—both seedlings of Cox's Orange parentage—gave a much larger proportion of sulphur shy seedlings with Rote Sommer Apfel than did the cross with Cox's Orange Pippin itself.

Table V.

Proportions of sulphur shy seedlings in families of which Rote Sommer Apfel was one parent.

Parents.	No. of seedlings.	% defoliated.
St. Cecelia	17	29
White Transparent	6	17
St. Everard	13	15
Cox's Orange Pippin ..	39	8
Stirling Castle	6	0
Devonshire Quarrenden ..	117	0

The fact that the very small family from the cross with Stirling Castle gave no sulphur shy seedlings is probably due to chance.

The remaining families present no features of unusual interest.

DISCUSSION.

The most recent researches have tended to show that, in breeding, the apple behaves as a complex polyploid. Investigations on the inheritance of such characters as fruit colour and shape among cultivated varieties (Crane and Lawrence, 1933), on certain vegetative characters among the so-called Paradise apples (Tydeman, 1933, 1935), and on immunity from attack by Woolly Aphis among seedlings from Northern Spy (Crane, Greenslade, Massee and Tydeman, 1936), have all pointed to the conclusion that many of the characters of the apple segregate in such a manner that selfing or crossing gives rise to progenies varying by very small gradations of difference in which class intervals are extremely difficult to delimit. This is thought to be due to the existence of reduplicated factors which, on recombination, give rise to small continuous differences. In the few cases in which a much simpler type of character segregation has been observed, as in the inheritance of pigmentation in crosses between green and purple apples (Lewis and Crane, 1938), these results are not difficult to reconcile with the theory of polysomic factors. The cytological evidence has amply confirmed the results of breeding. The apple has been shown to be a secondary polyploid (Darlington and Moffett, 1930; Moffett, 1931).

The evidence presented in this paper on the inheritance of sulphur shyness

in apple seedlings appears to be quite in accord with the trend of the main body of research on apple genetics. It is evident from Table I that the ten varieties most extensively used as parents in these crosses gave rise to families in which the proportion of sulphur shy seedlings varied within extremely wide limits, suggesting that those varieties transmitted susceptibility in different degrees. While families from Stirling Castle showed a much larger proportion of seedlings intolerant to sulphur, as would have been expected from the much greater susceptibility of the parent variety, the proportion of sulphur shy seedlings in these families showed very great variation from one family to another, according to the relative genetic constitution for sulphur shyness of the other parent.

The simplest explanation of these results is the one already advanced to explain the inheritance of numerous other characters of the apple, viz., that the expression of this character is controlled by a number of genes. This would explain the great diversity of degree of susceptibility known to exist among apple varieties themselves and the fact that, on breeding, such very different ratios of sulphur tolerant to sulphur shy seedlings are obtained when the same variety is crossed with a number of others.

Crane and Lawrence (1938) mention an interesting analogous case of the inheritance of susceptibility to sulphur damage among gooseberry varieties. Unpublished researches by Bailey showed that offspring from certain varieties were defoliated by sulphur sprays. Where Pitmaston Greengage was selfed a ratio of 3 sulphur tolerant to 1 sulphur shy seedlings was obtained, suggesting that the sulphur shy character was a pure recessive, inherited according to a simple Mendelian pattern. With other varieties, however, the ratios were more nearly 2 : 1.

It is evident that a fairly clear cut segregation for sulphur shyness may be expected in crosses between apple varieties. It should therefore be possible for the breeder to eliminate the undesirable individuals in the first generation. Although the extent of defoliation in the seedlings under discussion varied within wide limits, from ten per cent. to more than sixty per cent. of the foliage being lost, it was usually severe enough to affect seriously the growth and cropping of the tree. In most cases, such seedlings, however desirable as new varieties in other respects, would have little chance of introduction as commercial varieties, simply because they were sulphur shy. In crosses between even the most susceptible varieties, however, the breeder can look for a proportion of seedlings completely tolerant to sulphur sprays.

ACKNOWLEDGMENT.

The writer's thanks are due to Mr. T. N. Hoblyn for his statistical analysis of the foregoing data and for his advice as to their presentation.

SUMMARY.

Details of the reaction of seedlings from crosses between numerous apple varieties to spring applications of sulphur compounds for controlling Scab are given.

Where the highly susceptible variety Stirling Castle was used as a parent, the proportion of sulphur shy seedlings was usually high, but it varied according to the other variety used as parent.

Families in which White Transparent, Cox's Orange Pippin and Rote Sommer Apfel were used as one parent contained on the average from 7 per cent. to 54 per cent. of sulphur shy seedlings, but in the individual families great variation was found. With most of the other varieties used as parents, there was only a small proportion of sulphur shy seedlings in the families.

It is concluded that sulphur shyness in apples is controlled in inheritance by genetic factors and that a number of genes are involved.

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APPENDIX A.

Showing the Reaction to Sulphur Sprays of Apple varieties used as Parents.

Since many of the varieties used as parents in these crosses are not now extensively grown, little is known of their reaction to sulphur sprays. The following list has been compiled from information kindly supplied to the writer by several members of the staff at East Malling, and is given in the hope that it may prove of assistance in interpreting the genetical results. They desire to emphasize that the observations were frequently somewhat cursory, often limited to a single season and on material of very diverse character.

American Mother	Not damaged.
Bascombe's Mystery	No information.
Baumann's Red Reinette	No information.
Beauty of Bath	Susceptible.
Blenheim Orange	Not damaged.
Brownlee's Russet	Not damaged.
Christmas Pearmain	No information.
Cox's Orange Pippin	Rather susceptible.
D'Arcy Spice	Not damaged.
Devonshire Quarrenden	No information.
Early Mc'Intosh	No information.
Egremont Russet	Not damaged.
Ellison's Orange	Not damaged.
Golden Delicious	Slightly susceptible.
Golden Russet	No information.
Irish Peach	Not damaged.
Lady Carrington	No information.
Laxton's Superb	Slightly susceptible.
Mc'Intosh Red	Not damaged.
Northern Spy	Slightly susceptible.
Reinette Zuccamaglio	Not damaged.
Rome Beauty	Not damaged.
Rote Sommer Apfel	Rather susceptible.
St. Cecelia	Very susceptible.
St. Everard	Slightly susceptible.
Stayman Winesap	No information.
Stirling Castle	Very susceptible.
Wagener	Not damaged.
White Transparent	Slightly susceptible.
Winter Sunshine	Not damaged.
Worcester Pearmain	Not damaged.
Yellow Ingestrie	No information.

APPENDIX B.

Giving details of the Parentage of the Families with actual number of Sulphur Shy Seedlings.

	Total number of Seedlings.	Number defoliated.
Stirling Castle × Brownlee's Russet	69	8
Stirling Castle × Golden Russet	18	6
Stirling Castle × Lady Carrington	11	8
Stirling Castle × Rote Sommer Apfel	6	0
Stirling Castle × Yellow Ingestrie	8	3
Brownlee's Russet × Stirling Castle	29	4
Cox's Orange Pippin × Stirling Castle	5	2
Devonshire Quarrenden × Stirling Castle ..	154	32
Yellow Ingestrie × Stirling Castle	52	9
Cox's Orange Pippin × Blenheim Orange ..	4	1
Cox's Orange Pippin × Ellison's Orange ..	5	0
Cox's Orange Pippin × Rote Sommer Apfel ..	39	3
Bascombe's Mystery × Cox's Orange Pippin ..	21	1
D'Arcy Spice × Cox's Orange Pippin	5	0
Golden Delicious × Cox's Orange Pippin ..	14	0
Laxton's Superb × Cox's Orange Pippin	57	1
Rome Beauty × Cox's Orange Pippin	4	0
St. Everard × Cox's Orange Pippin	12	0
Winter Sunshine × Cox's Orange Pippin	35	4
Golden Delicious × St. Everard	68	0
Golden Delicious × Worcester Pearmain	10	0
Stayman Winesap × Golden Delicious	8	0
White Transparent × Golden Russet	68	4
White Transparent × Rote Sommer Apfel ..	6	1
Brownlee's Russet × White Transparent	15	1
Devonshire Quarrenden × Early McIntosh ..	143	2
Devonshire Quarrenden × Golden Russet.. ..	108	6
Devonshire Quarrenden × Rote Sommer Apfel ..	117	0
Devonshire Quarrenden × Worcester Pearmain ..	31	0
Devonshire Quarrenden × Yellow Ingrestrie ..	107	2
Brownlee's Russet × Devonshire Quarrenden ..	26	0
Ellison's Orange × Devonshire Quarrenden ..	41	0
Golden Russet × Devonshire Quarrenden.. ..	31	1
Stayman Winesap × Devonshire Quarrenden ..	38	2
Mc'Intosh Red × Beauty of Bath	12	0
Mc'Intosh Red × Golden Delicious	20	0
Mc'Intosh Red × Irish Peach	24	1
Mc'Intosh Red × Wagener	25	0
Mc'Intosh Red × Worcester Pearmain	26	0
Yellow Ingestrie × Brownlee's Russet	15	2
Yellow Ingestrie × Golden Russet	79	1
Rote Sommer Apfel × St. Everard	13	2
St. Cecelia × Rote Sommer Apfel	17	5
Brownlee's Russet × Christmas Pearmain ..	15	0
Baumann's Red Reinette × Brownlee's Russet ..	21	0
American Mother × Worcester Pearmain ..	16	1
Beauty of Bath × Blenheim Orange	6	0
Laxton's Superb × Egremont Russet	8	0
Northern Spy × Reinette Zuccamaglio	13	0
Rome Beauty × Worcester Pearmain	7	0

(*Received* 10/3/41)

THE JONES-BATEMAN CUP FOR RESEARCH IN FRUIT-GROWING

The following announcement is published at the request of the Royal Horticultural Society.

In 1920 Miss L. Jones-Bateman, of Cae Glas, Abergele, presented to the Royal Horticultural Society a valuable silver-gilt replica of the Warwick Vase to be used for the encouragement of fruit production. It is accordingly decided to offer it triennially for original research in fruit culture which has added to our knowledge of cultivation, genetics, or other relative matters.

Candidates should submit accounts of their work by October 31st. The work dealt with should have been mainly carried out by the candidate in the United Kingdom, and mostly during the past five years. The cup will be held for three years by the successful candidate, who must give a bond for its safe return. The holder will be eligible to compete on the next or any succeeding occasion. When the cup is relinquished the holder will receive a Hogg Medal.

The assessors will be three (two appointed by the Royal Horticultural Society and one by the National Farmers' Union), who will report to the Council of the Society upon the originality and comparative potential value to the fruit-growing industry of the work of the candidates.

The Council of the Royal Horticultural Society will award or withhold the Cup at its discretion.

REVIEWS

PLANT GROWTH SUBSTANCES. By HUGH NICOL. Second Edition. (Leonard Hill, Ltd., London, 1940, pp. xii.+148. 6 figs. 7s. 6d. net.)

The first edition of this book proved very useful in that it collected and collated a great amount of information into a small space and made it available at a very small price. It received at the hands of reviewers much praise, mixed with some criticism, mostly on the grounds of a lack of balance between the chemical and the phytological aspects of the subject. It is perhaps unusual to find an author who takes criticism in such good part, realizes that it is meant only constructively and thereupon endeavours to meet the reviewers' objections. In this second edition, most, if not all, of the chief criticisms have adequately been met.

The work is still frankly chemical in approach ; this, in fact, constitutes its great value. At the same time the chemical have been linked with the physiological and botanical aspects, and the whole now presents the balance that was lacking in the first edition.

A good deal of new material has been added, especially on the phytological aspects of the vitamins and their relations to the auxins and synthetic growth-substances, while extensive rearrangements of the text have been made. The lists of references have been brought up to date ; in this connection the very careful selection of key references from the truly vast amount of literature of recent years on the subject will be of great value to the student or investigator.

The first edition, in its format and price, was possibly experimental ; the author and the publishers are now apparently satisfied that the book has passed its trial run and is worthy of a better binding and a consequent higher price. With this conclusion the reviewer cordially agrees ; the book is unique in approach and content, and he looks forward to a long career for it in successive editions, which will be made necessary by the rapid advances which are almost daily being made in this most illuminating and revolutionary branch of plant study.

R.H.S.

TEXTBOOK OF GENERAL HORTICULTURE. By J. C. SCHILLETER and H. W. RICHEY. (McGraw-Hill Publishing Co., London, 1940, pp. viii. +367 ; 136 figs. 21s. net.)

Although there is an immense number of books on the art of horticulture, there is a great lack of general works on its science. Perhaps this is not so surprising when it is realized that the application of science to the oldest of the arts is of comparatively recent growth. Many excellent scientific works on specialized branches of horticulture, especially fruit-growing, have appeared, but this is one of the first attempts to give in one book a résumé of the whole field of horticultural production in relation to scientific knowledge.

The attempt is an excellent one, but a field so vast requires a larger volume than the present work to do it justice. The endeavour to miss nothing of importance has involved such drastic curtailment of detail that the book becomes little more than a general outline. The whole subject of plant nutrition and manuring, for example, is disposed of in seven pages, and the propagation of fruit trees in four. Incidentally, in this last example, the raising of seedling stock alone is dealt with, no mention being made of vegetatively-propagated clonal stocks, an astonishing omission even in an American book. It is unfortunate that the authors have attempted to be so comprehensive as to include

fifty-seven pages on pests and diseases (all grouped as "pests") and their control. The treatment is inadequate and the space might more usefully have been employed in enlarging the remaining sections.

The main criticism to be levelled at the book, however, is its exclusively American outlook. The instance already quoted is only one of many examples of complete omission of references to European, and especially British, work. This is reflected in the bibliographies at the end of each chapter which refer almost entirely to American books and papers.

With these reservations in mind, however, the book remains a useful one for the student to read as a general background.

R.H.S.

MODERN APPLE TREE PRUNING. By C. R. THOMPSON. (Headley Brothers, 109 Kingsway, London, 1941, pp. 47. 1s. 6d.)

This booklet is an expansion of articles intended chiefly for commercial apple growers, which appeared originally in the *Fruitgrower*. The author deserves much credit for his courageous attempt to condense so complex a subject into less than fifty pages. As Mr. Bush points out in his Foreword, the result may seem involved, at least to the beginner with everything to learn. Even experienced growers might be forgiven if they grudged the time needed to become familiar with the methods described ; but they will find the time well repaid. The author faces not only the necessity of allowing for the many factors which govern pruning—such as age, variety, condition and past performance of tree—as well as the influence of local conditions, but also tries to condense his various methods to rules of thumb, such as can be applied by the often untrained help which growers are now compelled to use. The complexity arises from the fact that different rules of thumb are needed for each age, vigour, performance and (in later years) variety group. Though the author follows the usual practice in dividing his subject matter primarily into age groups, in other respects his treatment is mainly original. In his first age group, "the young tree", he insists on certain consideration still too often ignored and, indeed, not only by inexperienced growers. Such are, the correct spacing of branches, neither too closely nor too widely, the impossibility of getting an adequate yield per acre before the trees cover a considerable proportion of the space allowed ; and the fact that leader tipping makes a tree smaller and is therefore unsatisfactory as a means of restoring vigour to weak young trees. In this last instance he very sensibly recommends deblossoming as an aid to the effects of improved cultivation and manuring. The remainder of the booklet discusses the pruning of mature trees, of aged and crowded trees, and the relation between pruning and irrregular bearing. In each case the author tries to provide rules which can be given to pruners of little experience, to keep them at least somewhere near the correct treatment. The booklet is made needlessly difficult to read by somewhat hasty writing. In one or two places the meaning is not clear, even after repeated reading. More than once, also, "pruning" is used interchangeably with "tipping". It is to be hoped that if a second edition is called for, and still more if the author carries out his promise to write a pruning manual, he will exercise greater care in his wording, so as to make the meaning unmistakably clear. These slight blemishes should not deter growers from getting and using the booklet.

N.H.G.

STUDIES IN FRAMEWORK GRAFTING OF MATURE FRUIT TREES

II.* APPLES

By R. J. HILTON†

INTRODUCTION.

THE accumulated knowledge and experience of the past thirty years has revolutionized the planning and management of the commercial orchard. Many varieties hitherto grown have turned out to be unsuitable for market requirements, local conditions, and the common routine of spraying and manuring. The planting of large blocks of a single variety, or of intermixed varieties often so closely that in the process of thinning they became reduced to a single variety, has been found to be unsatisfactory.

To-day there is a general movement to reduce the number of varieties on the market, to standardize them and the methods of culture, so that culinary and dessert sorts are segregated, and varieties demanding peculiar spraying and manuring schedules are either discarded or grown separately.

While these tendencies are all to the good, growers have been apt to forget the necessity of keeping a chosen intermixture of varieties, which exact experiment has proved over and over again to be essential for the vast majority of sorts, and desirable for all.

All these developments especially affect maturing orchards, the crops from which the grower has been long anticipating. He now needs to make a rapid change over which will rectify past miscalculations without too much delay, and his choice lies between grubbing and replanting or some sort of re-working or topgrafting.

Topworking and frameworking. In the past, fruit growers have been accustomed to graft mature trees by topworking, i.e. topgrafting methods. In brief the process consists of cutting back the main scaffold branches very nearly to the trunk, and inserting one or more scions into each cut end. It is obvious that by this method, not only has the framework of the trees to be entirely rebuilt, but the root system of the tree must adjust itself to a relatively very small top in the first few seasons after grafting. Garner and Walker (1938) pointed out that with topworking methods, " as much as ten years, according to variety, may be required before the tree returns to profitable cropping ".

* No. I of this series was entitled " A method of converting unprofitable fruit trees," by R. J. Garner (1934) who initiated these studies in Frameworking.

† Investigations undertaken at East Malling Research Station, Kent, England, during a period of study there in 1938 and 1939 as a Research Student from Macdonald College, Quebec.

These, and other disadvantages, have resulted in the development of a much more rapid method. This is known as frameworking, so-called because methods of grafting are involved which retain and refurnish the complete framework of the tree. In preparing a tree for frameworking only the *ends* of the scaffold branches together with some laterals and spurs are removed, the remainder being the framework upon which the scions are grafted. Although a few early horticulturists, notably T. A. Knight (1841), have made reference to the possible employment of such a process, it was not until less than two decades ago that it became adopted commercially. It was first used on a large scale in Tasmania (Thomas, 1928, 1930; Thomas and Raphael, 1933), and then in Victoria (Walker, 1935; Ward and Prescott, 1937), where infection of the large wounds incidental to topworked trees by the disease known as Papery Bark Canker (said to be due to *Polystictus versicolor*) was the cause of its adoption. Trees so treated showed such an early return to profitable bearing that the use of the method soon spread to England (Garner, 1934), South Africa (de Wet, 1936) and Canada (Collins, 1939).

Factors important in frameworking. Obviously many more scions are inserted on a tree by frameworking than by topworking, and this has made necessary the study of the whole subject of grafting and budding in special relation to frameworking.

Experiments were started at East Malling in 1932 to see whether frameworking was adaptable to English conditions and to compare its relative merits with those of topworking. As a result of the great promise of frameworking methods shown in this original comparison, more intensive investigations were begun in 1938 into method and type of grafting and the best periods for this operation. At the same time the possible influence on the new scion variety of the relatively large amount of intermediate framework was investigated.

The series of experiments described here was designed to study the relative efficiency of the chief frameworking methods in use in England and other fruit growing countries, and their effect on the growth and cropping of apples.

Framework grafting methods.

In this series of experiments, four methods of framework grafting have been employed, stub, side, inverted L and awl. The first two are cleft methods; that is, the scion is inserted in a cleft in the wood of the frame-intermediate. Inverted L and awl methods, on the other hand, are bark and rind methods, and the scion is inserted between the bark and the wood, so that no cleft in the latter is made. The differences in the methods of inserting the scions in these types of grafting are fully illustrated and explained by Garner and Walker (1938), but a brief outline is given below. Letters in parenthesis refer to the diagram (Fig. 1).

Stub grafting. Small lateral branches (up to 1 inch in diameter) which arise from the framework are cut at the base (B) in such a way as to retain a wedge-shaped scion base (A) by the grip of the wood. The lateral is then cut off directly over the scion base (C) leaving the scion firmly gripped in the remaining stub.

Side grafting. A cut is made into the wood of the scaffold branch and a scion with a basal wedge-cut (A) and (B), longer than that of a stub-graft scion,

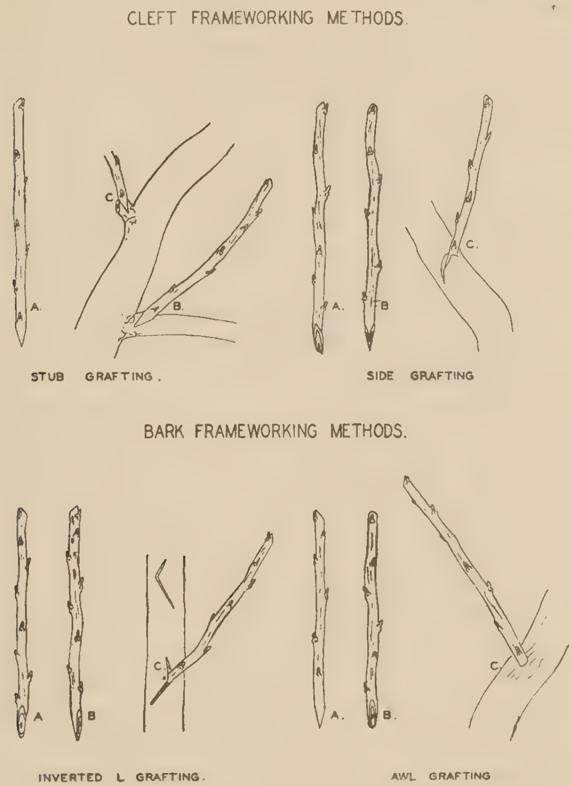

FIG. 1. Frameworking methods used in the experiments described.

is inserted either by bending the branch to open the cut, or, on larger limbs, by pushing the scion into the cleft (C) by force.

Inverted L grafting. The cut on the branch is made through the bark only to the cambial layer, and is shaped somewhat like an inverted L (C), but having an angle much greater than a right angle. The scion is cut with a through slanting stroke on the front side (A) of its base, and with a thin slice off the bark on the other side (B), to expose the cambium, so that union may take place along two exposed cambial surfaces. The scion, when firmly inserted between the

bark and wood, is held in place with a small nail. This was the only framework method used in which the scion required to be held in place artificially.

Awl grafting. The incision in the branch is made with a bent, sharpened, tool (such as a bent awl). This is inserted more or less at right angles to the branch, so that the curved blade follows the contour of the branch between the bark and wood for a short distance. The scion base is cut wedge shaped (A) and (B) so that when it is in place (C), union should normally take place along two exposed surfaces.

In all these grafting methods a mastic is necessary, and a single standard grafting wax was used. This has been described by Garner and Walker (1938), and it proved very efficient.

THE EFFECT OF TIME AND METHOD OF GRAFTING, AND LENGTH OF SCION.

The following investigation was designed to compare the four methods of framework grafting just described in relation to time of insertion and optimum length of scion.

Cardinall and Bradford (1929), Middleton (1928), and Vincent and Luce (1928), state that for topgrafting, the work should be done early, except in fruit areas where exceptionally cold weather might cause injury at the graft-unions. Garner (1936) found that satisfactory results could be obtained in the south of England from February to mid-July, and recommended the period March-April as that in which the grafting is most successful. Various writers on frameworking, however, in addition to those already mentioned, do not make definite recommendations as to the best time to graft, but state that bud-break is generally considered to be the most effectual time, although the period in spring when labour may best be spared for grafting is often the determining consideration (Leishman, 1936, and Wicks, 1937).

Most writers on topgrafting recommend a short scion (2-4 buds). Developments in frameworking are so recent that the literature on the subject is limited, but Garner and Walker (1938) regard scions with 6-8 buds as the best. For the peg or plug method, as used in Australia (Leishman, 1936, Thomas and Raphael, 1933), short scions (2-4 buds) are used. This method, in which scions are driven into chisel cuts on the branch, is not yet generally recommended.

OUTLINE OF EXPERIMENTS.

Experiments were designed in the spring of 1938 to test these points. The material used throughout consisted of 22-year-old trees of Mr. Gladstone on mixed rootstocks mostly M.II, with some M.III and M.V. The scion used was Worcester Pearmain.*

* Hereinafter, when reference is made to a specific scion/intermediate combination after it has been first mentioned, the names will be abbreviated where desirable, and the combination will be designated Worcester/Gladstone, with the scion variety always written first.

All the trees were prepared for frameworking in the same way, and the distance between scions on the scaffold was always about 10 inches.

Time of grafting and length of scion in relation to methods of:

(*a*) *framework cleft grafting.* Twenty of the selected trees were grouped into sets of four, and one set was grafted each month from February to June inclusive. Of each set, two trees were grafted with long scions (8 buds) and two with short scions (4 buds); and on each tree approximately one-half of the scions were stub and one-half side grafted.

(*b*) *framework bark grafting.* This series of twenty trees was similar to the above, but the inverted L and awl bark grafting methods were used. Since these methods cannot be used until the bark slips or peels easily, only three months, April, May and June, were compared.

Direct comparison of framework cleft and bark grafting on the same tree. Twelve further trees were grafted in late April. Each of these received one of the four possible combinations of one cleft and one bark method on each tree, with the object of testing the interaction of the two methods when used on the same tree. The scions used had from 7-10 buds each throughout. The treatments were triplicated.

Source and condition of scion wood. Most of the Worcester Pearmain scion wood was obtained during the winter of 1937-38 from a single experimental plantation at East Malling. A few scions, however, came from an orchard at Kirdford, West Sussex. These were intermixed and all were heeled in in soil, out of direct sunlight until the beginning of May, when those which remained were moved to low temperature storage at about 40° F., to maintain dormancy. Throughout the five months of grafting operations, the scion wood remained in excellent, sappy condition, and no shrivelling was noted.

Experimental design. In the main experiment each combination of method, time and scion length was duplicated in two blocks. To increase the accuracy of the comparison of scion length, which might be expected to show the smaller difference, the twenty trees in each block were subdivided into ten pairs of trees as similar as possible. Each pair was treated alike except for the length of scion used. On each cleft grafted tree, the stub and side grafts, and on each bark grafted tree, the inverted L and awl grafts, were approximately equal in numbers. Thus the design could be regarded as two randomized blocks in which the primary unit was a pair of trees. Each replicate (plot) of two trees for each time of grafting could be split into units of one tree for comparisons of scion length, and further split into half-tree units for comparisons of method. This method of arrangement is known as a split plot layout (Yates, 1937).

The subsidiary experiment to test any possible interaction of cleft and bark grafting methods on the same tree was designed in three straightforward

randomized blocks, each block containing four trees, each of which had one of the four possible pairs of cleft and bark grafts.

Records. On every tree the number and take of scions was recorded, whilst fruit bud counts and growth measurements were made separately for each individual scion. It was decided to use complete shoot measurements primarily to estimate the vigour of the trees in the first two years after grafting. Girths of trunk were measured at the start of the experiment and each year subsequently. After the measurement of new growth had become impossible, trunk increment had to be used as the measure of vigour.

Worcester Pearmain is a variety which normally forms axillary fruit buds freely on one-year-old wood. With this variety, therefore, it is common for fruit buds to develop, and in some instances actually to set fruit on the original scion *in the year of grafting.* The fruit buds which flowered in 1938 and the number and weight of fruit which matured were recorded. Fruit buds were also counted in 1939, and the crops in 1939 and 1940 were recorded.

Since the trees were not uniform in size, in order to eliminate the effect of the variable number of scions on a tree, the total shoot growth and number of fruit buds and fruits *per scion* were used in the analyses of the results.

Statistical analysis of results. The analysis of variance, adapted for use with the split plot design here used (Yates, 1937), was employed. The main departure from the analysis as carried out in a straight randomized block experiment was its division into three parts, each of which had a separate estimate of error. Thus, where times of grafting were compared, the unit was two trees; comparisons of length of scion were made on single trees, and of kind of graft on half-tree units. Thus, for example, it might be expected that the error of a comparison within a single tree would be less than that of whole trees scattered at random over the plantation.

The significant differences shown in the Tables which follow were calculated by using the "t" test, "t" being the ratio of any particular difference to its standard error.

Results.

Cleft grafting methods.

(i) *Percentage take of scions.* The general mean percentage take for the forty half-trees was 96·7, and in no case was it below 89·6. This was very satisfactory, particularly considering the unusually dry weather in March and April 1938. As the difference between treatments was obviously so small as to be of little importance no statistical analysis was made.

(ii) *Fruit buds in 1938.* Those buds which developed normally on the original scion wood after the grafting had been done were counted in 1938,

but not separately for each grafting method. It is, therefore, possible to compare only the effects of the five times of grafting and the two lengths of scion.

Table I.

Average number of fruit buds per scion. Cleft grafted Worcester/Gladstone—1938.

	February.	March.	April.	May.	June.
Mean no. of fruit buds per scion	·30	·46	·38	2·14	·77

Significant differences (P = ·05) = ·26 ; (P = ·01) = ·41.

It is clear from Table I that the scions grafted in May developed definitely more fruit buds than those grafted at any other time. Those grafted in June had more fruit buds than those in February, March or April, but between the three latter months there was no significant difference.

No significant differences were found for the number of fruit buds per scion between the two lengths of scion in any month.

It would normally be expected that the long scions would develop more fruit buds than the short, but this was not so. This may have been due to some varietal or nutritional factor as yet not fully understood, such as the premature dropping of axillary fruit buds well known on Worcester Pearmain.

(iii) *Yield in* 1938. The fruit from these trees was harvested from four to eight months after they were grafted, depending on the date of grafting, so it is not surprising that the crop was not of commercial importance. The trees grafted in May, however, bore an average of ten pounds per tree of small but fair to good quality fruits. This was much higher than the crop borne on trees grafted in any other month.

With apple varieties not having the Worcester Pearmain habit of axillary fruit bud formation, the first season's crop would probably have been negligible.

(iv) *Wood growth during* 1938. The average wood growth in cm. per scion for all treatments is shown in Table II.

The last column shows definitely that the later the grafting is undertaken the less new growth results ; in fact, there is a continuous diminishing range from February, 88·7 cm., to June, 24·7 cm. Further, on the average, long scions made more wood growth than short ones, but this was entirely due to the early grafted trees, for in May and June the short scions made more wood growth than the long.

The consistently large difference found between wood growth on stub and side grafted scions is also significant.

TABLE II.

Average wood growth per scion in centimetres. Cleft grafted Worcester/Gladstone
—1938.

Month.	Long scions.		Short scions.		Mean for month.
	Stub.	Side.	Stub.	Side.	
February ..	148·1	69·0	88·9	49·0	88·7
March	112·3	63·5	80·8	33·4	72·5
April	91·9	47·7	72·0	26·9	59·7
May	43·8	17·1	88·1	30·3	44·8
June	29·6	10·4	43·0	17·0	24·7
Means	85·1	41·5	74·6	31·3	
	63·3		52·9		

Significant difference for months (P = ·05) = 35·0 cm.; (P = ·01) = 47·5 cm.
The means which are not significantly different are bracketed together.

TABLE III.

Average number of fruit buds per scion. Cleft grafted Worcester/Gladstone—1939.

Month.	Long scions.		Short scions.		Mean for month.
	Stub.	Side.	Stub.	Side.	
February ..	1·69	2·10	1·30	2·38	1·86
March	2·39	2·49	1·24	1·75	1·97
April	2·78	3·03	1·33	1·70	2·21
May	2·26	2·13	1·53	1·42	1·83
June	2·37	2·88	1·37	2·11	2·18
Means	2·30	2·53	1·35	1·87	2·01

(v) *Fruit buds in* 1939. The fruit buds initiated on the first season's wood growth were counted in the spring of 1939 and are summarized in Table III, which gives that season's fruit buds per scion.

The following are the outstanding results:

(i) There was no significant difference between any of the five months of grafting.

(ii) Long scions gave significantly more fruit buds per scion than short scions in all months.

(iii) Side grafts produced definitely more fruit buds on each scion than stub grafts, except in May, when the reverse was true.

Referring to (i), in spite of the fact that there was no significant difference due to time of grafting, the number of fruit buds per scion in 1939 on the May grafted trees was least for all the months, this being the month which developed far more fruit buds in the season of grafting. The actual differences, however,

were not great, and when the crop harvested in this year is considered it will be found that the May grafts set an exceptionally high proportion of their blossoms.

(vi) *Tree growth subsequent to* 1938. It was possible to continue wood measurements of whole trees in 1939. During that year there was a tendency, specially marked in the short scions, for the comparative growth of the grafts made at different times to even up. While the earlier grafted trees continued on the whole to make more growth, the difference in their favour was very greatly reduced. The difference between long and short scions in the earlier months was still maintained. For the 1940 growth the measurement of girth had mainly to be relied upon, and this suggested a further evening up of growth. Visual records of wood pruned off in the spring of 1941 further confirmed this impression.

(vii) *Yield subsequent to* 1938. The comparative cropping of the cleft grafted trees is summarized in Table IV.

TABLE IV.

Crop, in lb. per 100 *live scions, of cleft grafted Worcester Gladstone trees*—1938-40.

Grafted in :	Long scions.				Short scions.				Mean long and short grafts.
	1938.	1939.	1940.	Total.	1938.	1939.	1940.	Total.	
February ..	0	32·3	9·0	**41·3**	0·1	30·7	6·1	**36·9**	**39·1**
March ..	0·3	42·9	21·9	**65·1**	0	21·9	11·1	**33·0**	**49·0**
April ..	0·9	39·4	25·1	**65·4**	0·2	27·8	13·4	**41·4**	**53·4**
May ..	8·5	49·1	37·0	**94·6**	5·4	36·4	23·7	**65·5**	**80·0**
June ..	0·9	43·4	14·6	**58·9**	0·6	23·4	19·7	**43·7**	**51·3**
Means ..	**2·1**	**41·4**	**21·5**	**65·0**	**1·3**	**28·0**	**14·8**	**44·1**	**54·5**

The crops are assessed by the weight of fruit in pounds per 100 live scions. While, owing to variation in the number of scions inserted in each tree, this is the only accurate measure for comparison, it is interesting to record that during the first three years after grafting, individual trees bore anything from one to three bushels (120 lb.) per tree.

The most striking points shown are the outstanding performance of the May grafted trees throughout the three years and the consistent superiority of the long scions over the short.

If the evening up of growth is maintained, it seems likely that differences in cropping will tend to disappear, although the indications are that, up to the present, the differences are due rather to a higher blossom set than to a greater number of fruit buds. Observations on amount and position of blossom trusses were made in 1941. These suggest that the trees were then all blossoming heavily and in very much the same way.

Bark grafting methods.

(i) *Percentage take of scions.* As with the cleft grafts, the average take was a high one (96·3%). The takes of scions grafted in April, May and June were 93%, 97%, and 99% respectively. As with the cleft grafted scions also, slightly more scions grew successfully on trees grafted late in the season.

(ii) *Fruit buds in* 1938. Neither the time of grafting nor the length of scion significantly affected the number of fruit buds per scion in the year of grafting (Table V).

TABLE V.

Average number of fruit buds per scion. Bark grafted Worcester/Gladstone—1938.

	April.	May.	June.	Mean.
Long scions	·29	1·22	·84	·78
Short scions	·42	1·19	·62	·74
Means	·36	1·21	·73	·76

Certainly there are some interesting differences between months, similar to those found with cleft grafts, but as these differences are not significant no definite conclusions can be drawn.

In comparison with the cleft grafts, while the numbers of fruit buds were alike in April and June, only about half developed in May.

(iii) *Yield in* 1938. The crop in the season of grafting was less than that of the cleft grafted trees. May scions again showed the largest yield, the trees bearing an average of slightly more than 3½ lb., but the crop on April and June scions was very small.

(iv) *Wood growth during* 1938. The records of wood growth in 1938 confirm those for the cleft grafted scions in that those grafted earliest made the most growth ; thus the growth of the scions grafted in April averaged 33·5 cm., whilst that of those grafted in June was only 13·2 cm.

As with cleft grafts, the short scions made more growth than the long ones in June, contrary to the general tendency. In every comparison except long scions in June, more growth was made on the inverted L grafts than on the awl grafts. The former averaged on the whole 26·8 cm. while the awl grafts made only 18·3 cm.

Subsequent to 1938 the same tendency to even up was observed as with the cleft grafts.

(v) *Fruit buds in* 1939. Time of grafting had no influence on the number of fruit buds per scion ; as with the cleft grafts, the long scions had significantly

more fruit buds than the short ones. There was no difference between the inverted L and the awl grafts.

(vi) *Yield subsequent to* 1938. There was no significant difference in yield due to time of bark grafting. Over the three-year period, April and June bark grafts yielded very much the same crops as the cleft grafts, but the superiority shown by the May cleft grafts was not repeated. Long scions again produced more crop than short ones, the relative crops per 100 scions being 65·7 lb. and 43·6 lb.

Cleft and bark grafts on the same tree. In refurnishing the framework of a mature tree, it would be an obvious advantage to graft each scion in the optimum position and to be able to use the most appropriate method of grafting for any particular position. In this subsidiary experiment, therefore, both cleft and bark types of grafting were intermixed on the same tree, just as the grower might wish to do in practice. Three replications of four combinations were tested as follows :

Stub and Inverted L.

Stub and Awl.

Side and Inverted L.

Side and Awl.

Records were made similar to those already described in the main experiment. In the two seasons under review, apart from the differences in vigour of growth due to the different types of grafting, as already observed, there was little or no evidence that one type of graft influenced the growth, fruit bud formation or cropping of another type on the same tree.

Comparison of framework budding with stub and inverted L grafting.

Framework budding has never become commercially important in England, but it is widely used in some fruit growing countries. In Australia, Orchard (1936), Thomas and Raphael (1933), Ward and Prescott (1937), and Wicks (1937) all state that budding into lateral shoots is a convenient method for the conversion of fruit trees to different varieties, and Thomas and Raphael stress the fact that this method promotes a very strong union of scion and frame-intermediate. The chief disadvantages are that the operation has to be done during summer, which is a relatively busy season, and, in comparison with other frameworking methods, a year is lost before the new variety becomes established. This is because suitable lateral growth has to be prepared by hard pruning a year beforehand, and the buds inserted in summer do not grow into laterals until the following spring.

Some 20-year-old Bramley's Seedling apple trees at East Malling Research Station had been framework budded in the summer of 1934 with Grenadier, and 41 per cent. of the buds had failed to grow. In the following spring the failures had been replaced by stub (cleft) and inverted L (bark) grafting. Of the scions inserted over 95 per cent. had grown, thus providing a series of Bramley's Seedling frames each of which, when examined, contained Grenadier buds as well as bark and cleft grafts all of three years' growth, and thus suitable for comparison.

Records. The wood growth in centimetres on each scion on four trees was measured, tracing back the 1937, 1936 and 1935 growth separately. Unfortunately, no allowance could be made for the wood growth that was pruned away in the first two years. It was observed, however, that more growth was cut from the stub grafted scions than from the budded scions. It was not possible to estimate whether the inverted L grafted scions had more or less growth pruned away than had the budded scions, but because of their lack of initial vigour they also had fewer prunings removed than the stub grafted scions. In addition to measurements of wood growth, the fruit buds in the spring of 1938 were counted.

(i) *Wood growth.* The unavoidably unequal numbers of scions necessitated a specialized statistical treatment to assess the significance of the differences shown, and the method suggested by Snedecor (1934) was used.

Table VI shows the mean growths per scion and the numbers of scions upon which the estimates are based. For purposes of calculating significant differences, the standard error of the growth of one scion is given.

TABLE VI.

Mean wood growth in cm. per scion and number of scions, Grenadier/Bramley.

Year.	Stub grafts.		Buds.		Inverted L grafts.	
	Mean wood growth.	No. scions.	Mean wood growth.	No. scions.	Mean wood growth.	No. scions.
1935	81·4	103	51·4	214	31·3	47
1936	21·4		21·1		20·2	
1937	50·4		40·6		23·7	

Standard Error of the growth of one scion = 53·0 cm.

The stub grafted scions made more growth than the buds, and the latter more than the inverted L grafts over the whole period, but the differences in 1936 were not significant. The fact that more wood was removed in pruning from stub grafts than from buds or inverted L grafts indicates that the actual differences in amount of growth between these treatments were even greater.

(ii) *Fruit bud formation.* The numbers of fruit buds in 1936 are given in Table VII together with the numbers per scion and the differences necessary for significance. From this Table it will be seen that though there was no significant difference between the total numbers of fruit buds produced by stub grafting and budding, the former produced many more per scion than the latter. Allowing for the number of scions, the inverted L grafts did not differ significantly from the buds.

TABLE VII.

Average number of fruit buds for each tree and for each scion. Grenadier/Bramley.

	Stub grafts.	Buds.	Inverted L grafts.	Sig. Diff. P = ·05
Number of scions (4 trees) ..	103	214	47	
Fruit buds per tree	353	402	69	209
Fruit buds per scion	13·3	7·6	5·7	3·4

If the number of fruit buds and the average growth of a scion are compared it will be seen that the proportion is much the same for the three methods. No special blossoming virtues can be attributed to any one method except in so far as there was a greater length of wood on which to form buds.

The effect of scion position on the frame on growth.

In setting out the grafts on a frameworked tree it is desirable to know whether the normal tendency of the topmost shoots of a tree to grow more strongly is likely to be repeated. If this were so it might be possible by adjusting the spacing, type of grafting or length of scion in different parts of the tree, to improve the general balance of growth and fruit bud formation.

With this in mind a series of measurements was carried out in the winters of 1937-38 and 1938-39. Already established frameworked scions were selected from the following sources : (*a*) twenty mature Lane's Prince Albert apple trees which had been frameworked in the spring of 1937 with Cox's Orange Pippin, ten by stub and ten by inverted L methods ; (*b*) four mature Bramley's Seedling apple trees which had been frameworked with Grenadier in 1934 by budding, and on which the bud failures had been replaced in 1935 by stub and inverted L grafts.

From each of the Cox/Lane trees, four main scaffold branches were selected in January 1938, and three of the same four in January 1939. Each selected branch bore a series of six or more scions along the branch, uninterrupted by laterals or crotch formations. Complications which might be introduced by the position and vigour of laterals or forked branches were thus eliminated. By

selecting scions arranged in this way it was possible to measure their wood growth and, by arbitrarily inserting a mid-point on the scaffold, to have at least three scions above and three below this mid-point.

(i) *The Cox/Lane grafts* (*two years*). On the stub grafted trees there was significantly more growth of the scions in the lower position in the first season after grafting. In the subsequent year, however, the relative growth difference was reduced to insignificance. In general the inverted L grafted trees showed the same tendency, but in neither year were the differences in themselves significant.

(ii) *The Grenadier/Bramley grafts* (*three years*). From Grenadier/Bramley trees which had been budded, stub grafted and inverted L grafted, only scaffold branches were selected which had at least six stub grafts distributed along a piece of scaffold that was clear of crotches or laterals. Thus the material was in this respect comparable to that taken from the Cox/Lane trees. From each of two of the four trees in the series, six such scaffold branches were selected, and four from each of the other trees. The mean wood growth for each position, and the difference necessary for significance ($P = \cdot 05$) are given in Table VIII.

TABLE VIII.

Effect of scion position on wood growth. Grenadier/Bramley.

Year.	Mean growth per scion in cm.			Diff. necessary for significance ($P = \cdot 05$).
	Above.	Below.	Difference.	
1935	196	173	23	
1936	90	46	44	42·9
1937	213	105	108	

Over the whole period there is a difference in favour of the upper scions. However, the differences were not alike in all three seasons, becoming significant only in the second season, and being more pronounced in the third.

With Cox/Lane, as already noted, the scions in the lower position tended to grow more strongly than those above them ; but the difference had actually decreased in the second season. In the light of the results shown above, it seems probable that the scions in a higher position on the scaffold branch do grow more strongly than those lower down, and that this effect becomes more pronounced in succeeding years.

Angle of branch incidence.

In commercial practice, in order to check lateral growth and induce fruiting, branches are often artificially bent away from the vertical. In conjunction

with the above observations an attempt was made to study the influence of the angle of branch incidence on scion growth. While no very definite results can be claimed, as was only to be expected, there was a tendency for the scions to make more growth when the scaffold branches were straighter.

It seems, therefore, that it may be worth while to take into consideration, not only the straightness of the limb but the angle at which the scion is grafted thereon. This may well determine whether it becomes a vegetative shoot or a fruiting lateral.

THE INFLUENCE OF THE FRAME INTERMEDIATE ON THE DEVELOPMENT OF THE SCIONS GRAFTED THEREON.

The fact that an intermediate piece between rootstock and scion can influence the character of either root or scion, has for some time been well recognized by horticulturists. Grubb (1939), using intermediates of 3 inches to 2 feet in length, observed that the longer the intermediate, the greater was its effect.

Again, it is a common practice in countries liable to extreme winter temperatures to double-work apple trees, using an intermediate variety known to be resistant to winter injury. This practice is also extended to include intermediates of known resistance to important diseases and insect pests. In all these cases, however, relatively immature trees have been used for investigation, and the practice of frameworking established ones raises the question of the influence of the intermediate where it is proportionally very large. An attempt was therefore made to follow up the behaviour of a single scion variety frameworked on a range of different established intermediates.

Material. A series of ten-year-old apple trees, frameworked with Cox's Orange Pippin in 1937 by stub and inverted L methods was available. Forty-five trees, including from one to four specimens of fifteen varieties,* were used. The trees were all on Malling V rootstock, with the exception of one on Malling II, two on Malling IX, and one on an unknown rootstock.

Records. The relative vigour for the first year after grafting was estimated by complete wood growth measurements of all trees at the end of the 1937 growing season, and for the second year (1938) by the number of shoots removed during pruning in the spring of 1939.

There was practically no blossom on any of the trees in 1938, but in 1939 an estimate was made by eye of the relative fruit bud production, the records being grouped into four classes.

* White Lion, Cockle's Pippin, Scarlet Nonpareil, Long Bider, St. Edmund's Russet, Ananas Reinette, Golden Russet, Ross Nonpareil, Christmas Pearmain, Aromatic Russet, Braddick's Nonpareil, White Transparent, Sturmer Pippin, Grand Sultan, Carter's Pearmain.

Results.

Percentage take of scions. The take of the Cox's Orange Pippin scions was almost uniformly good and showed no evidence of incompatibility between the scion variety and any of the intermediates.

Wood growth. (i) *Total growth per tree in* 1937. Very large and highly significant differences between the total growth made on the different intermediates were established. These varied from 84·0 metres on White Lion intermediate to 24·5 on Braddick's Nonpareil, both of which varieties were on Malling No. V rootstock. However, when the size of the original scaffold was taken into account by dividing the total growth by the number of scions inserted on each tree, no significant difference in growth per scion was found between any of the intermediates.

(ii) *Estimated growth per scion in* 1938. The number of shoots removed in pruning for each variety was divided by the appropriate number of scions. Although a considerably larger number of shoots per scion were removed in pruning from some varieties than others, no significant differences were obtained. There was, however, an indication that the influence of the intermediate on the growth of the scion might possibly become more pronounced in succeeding seasons.

During 1939 and 1940 the relative increments in cross section of stem showed that the scions on at least two varieties—St. Edmund's Russet and Braddick's Nonpareil—were growing more strongly than would have been expected from the previous vigour of the trees. On the other hand, the growth on one variety—Scarlet Nonpareil—was noticeably weak. The growth of the scions on Sturmer Pippin on No. IX rootstock was as dwarfed as the original intermediate.

Fruit buds 1939. The estimation of the fruit buds in 1939 was not detailed enough to permit an analysis to be made. It did indicate, however, that the most vigorous intermediates (such as White Lion and Scarlet Nonpareil) did not necessarily show the most bloom. The former showed an excellent amount of blossom, whereas on Scarlet Nonpareil intermediate the Cox's Orange Pippin scions had very few fruit buds. Long Bider, one of the intermediates producing the highest growth per scion, also gave an excellent show of fruit buds, whereas Christmas Pearmain, which gave a low amount of growth per scion, also had few fruit buds.

Several of the combinations had a later blossoming period than others. The intermediates which showed this effect on the scion variety were Christmas Pearmain, Ross Nonpareil, Aromatic Russet, Scarlet Nonpareil and Carter's Pearmain.

Fruit 1939 *and* 1940. The total crops harvested during 1939 and 1940 varied from 53 lb. on the dwarf trees on Sturmer Pippin on No. IX to nothing on

Aromatic Russet and Scarlet Nonpareil. Trees on White Lion which blossomed heavily were somewhat variable, but averaged 30 lb. per tree. The Cox's on two varieties noted for their vigour—St. Edmund's Russet and Braddick's Nonpareil—bore very little fruit.

While it must be borne in mind that the unit of trees was all too small and their arrangement unsuitable for exact comparisons, it is somewhat surprising that four years after grafting, this range of mature frames had not demonstrated a more marked influence on Cox's Orange Pippin.

DISCUSSION.

Whilst it was known that framework grafting was adaptable to a large range of climates, the above intensive studies have helped to settle a number of points of important detail under English conditions.

The most striking conclusion is that the method in general is amazingly flexible, at least as far as apples are concerned. Next to the rapidity with which a variety can be converted and a quick return to blossoming for cross pollination purposes obtained, perhaps the most important advantage is the length of the period during which the operation can be performed by the use of appropriate methods. Equally successful graftings have been made from February to June inclusive. Although the first crops from frameworked trees may not be of great importance, such trees undoubtedly do return to commercial cropping very rapidly.

Whilst by carefully selecting the different methods of grafting to be employed it is possible to some extent to encourage either vegetative growth or quick blossoming in the early years, trees frameworked by all methods return to a normal balance of growth and cropping very soon.

It was fully anticipated that different mature framework intermediates might have a considerable effect on the behaviour of the second scion variety. A preliminary study over the first four years has not, however, borne this out, though there seems to be more effect of the intermediate on blossoming than on vigour.

SUMMARY.

1. The advantages of the quick reworking of mature fruit trees are discussed and its adoption in various countries is summarized.

2. The four main methods of framework grafting, two cleft and two bark, are described.

3. An account is given of exact experiments with apples (Worcester Pearmain worked on Gladstone frames) comparing time of grafting and length of scion suitable for the above methods. There was no significant difference in percentage take between any of the methods.

Cleft grafting. Operations were carried out from February to June. At the start the *earlier* grafted trees made the most growth and in these, long grafts (eight buds) gave more growth than short ones (four buds). The growth of the stub grafts was strikingly more vigorous than that of the side grafts throughout. After three seasons there was a general tendency for growth to even up. The trees grafted in May developed more fruit buds in the first season than all the others, and though in the second year they produced slightly fewer, a higher proportion set fruit. In this and in the third season these trees were outstanding in their crops. The blossoming and crops of the remainder were alike. Long scions resulted in heavier crops than short ones. Within the first three seasons the actual crops per tree ranged from one to three bushels.

Bark grafting. It was possible to make bark grafts only from April to June. Whilst in general the results with regard to vigour and blossoming confirmed those of the cleft grafts, the differences were not so striking, and as a whole bark grafts were, at the start, much less vigorous than cleft grafts. Of the two types, the growth from inverted L grafts was more vigorous than that from awl grafts. Whilst the cropping of April and June bark grafts was very similar to that of comparable cleft grafts, that of the May bark grafts was not outstanding.

4. Methods of cleft and bark grafting were intermixed on the same tree and, apart from differences in vigour of growth due to the different types of graft already observed, there was little evidence of any interaction one with another.

5. In direct comparisons on the same tree, stub grafting resulted in more growth and more fruit buds than budding, which, in its turn, was superior to inverted L grafting.

6. An examination of the effect on growth of the position of the scion on the frame indicated that this was indeterminate in the season after grafting, but that apical dominance was likely to become re-established eventually.

7. The influence of fifteen ten-year-old framework intermediates on the vigour of Cox's Orange Pippin scions was not markedly different in the first four seasons after grafting. Differences in fruit bud formation and cropping were more noticeable.

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STUDIES IN FRAMEWORK GRAFTING OF MATURE FRUIT TREES

III. PLUMS

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In plums, just as in apples, the developments in modern commercial fruit-growing have created a demand for the rapid replacement of varieties which are for one reason or another uneconomic. Certain heavy cropping but poor quality early and mid-season varieties have been over-planted and there has been a demand for more high quality dessert and late maturing plums. The development of methods of frameworking plums has therefore become a matter of practical importance. In the present investigation the comparative merits of different methods of grafting are assessed.

A COMPARISON OF FRAMEWORKING METHODS.

The frameworking of plum trees calls for essentially the same procedure in the preparation of the trees and the methods of scion insertion as for apple trees. As Garner and Walker (1938) point out, however, the bark of plum trees is thinner than and does not peel as early in the spring as that of apple trees, and incompatibilities occur not infrequently within and between certain plum species. There are, therefore, certain minor variations in frameworking methods on the two fruits. Neilson (1927) states that grafting (topworking) may successfully be done on apples, pears and plums, but that peaches, cherries and apricots should be topworked by budding on lateral shoots. It is not generally recognized that plums can be topworked by grafting in the orchard with as much certainty as they can be budded in the nursery, because the exudation of gum from the wounds is sometimes regarded as a detriment in grafting mature plum trees (as it is known to be in some cherry varieties) and because the fungus that causes Silver Leaf disease, which is common in mature plum trees in England, enters readily through wounds. Frameworking plums may overcome this obstacle since the number of large wounds is greatly lessened, in comparison with top-working.

* Investigations undertaken at East Malling Research Station, Kent, England, during a period of study there in 1938 and 1939 as a Research Student from Macdonald College, Quebec. Since 1939 the observations have been carried on by the Recording Staff of the Station. The second author has analysed the results and completed the present paper.

The following experiment was planned to provide information as to the most effective frameworking methods, and the effect of them on the growth and cropping of good quality commercial varieties.

MATERIAL AND METHODS.

In the spring of 1938, twenty-eight standard Czar plum trees were selected for frameworking. This variety is a common one in the south of England; it is very prolific, but not of high dessert quality. Further, the fruit matures at a time when marketing is often difficult, so that, in recent years, there has been a definite demand from growers for information as to suitable varieties of better quality to replace it. The selected trees were part of a plum rootstock trial, and had been planted as two-year-olds in the winter of 1925-26. The cultural treatment had been uniform for the whole plantation.

The experimental arrangement was primarily in two blocks, each containing seven pairs of trees, each pair being frameworked with one of seven varieties. Within each pair, both members of which were as far as possible on the same rootstock, one tree had cleft and the other bark grafts. There were 60 grafts to a tree and equal numbers of the two kinds of cleft (stub and side) or bark (inverted L and awl) grafts were made on each. This arrangement and the modifications in statistical analysis pertaining to it have already been referred to (Part II, p. 154) and need not be further enlarged upon here.

The method of stub grafting made it necessary to use suitable stubs (of lateral branches or spurs) where they were available. It was not always possible, therefore, to arrange stub and side grafts alternately on the scaffold branch, although this was done where the position of suitable stubs allowed it. The two bark grafting methods were employed alternately along each scaffold branch, but only one method (inverted L) could be used as a limb-end graft, because awl grafting can be done only along the branches and not at the ends.

The seven scion varieties and the rootstocks of the Czar intermediates on which they were grafted were the following:

Scion varieties.	*Rootstocks of Czar Intermediates.*
Oullins Golden Gage	Myrobolan B and Brompton.
Ontario	Myrobolan B, Cambridge Gage and Blaisdon Red.
Jefferson's Gage	Myrobolan B and D.
Cambridge Gage	Common Mussel and Myrobolan C and D.
Warwickshire Drooper	Narrow Leaved Shiny Mussel.
Monarch	Broad Leaved Shiny Mussel.
Victoria	Common Mussel and Damas C.

The cleft grafting was carried out from March 23rd to 26th, and the bark grafting from April 4th to 6th, 1938. The latter dates were rather early for the bark to be in a peeling condition, but in 1938 the sap had been flowing for several days before the trees were bark grafted. The methods of stub, side and inverted L grafting were the same as for apples (Part II, p. 151), but the thin and brittle bark of the Czar trees made it necessary to modify the awl grafting method. Instead of forcing the scion into an opening made in the ordinary way for this method, a cut was made through the bark with the knife point at right angles to the desired direction of the scion, and a V-shaped section of bark was removed so that the scion would lie more closely to the branch and the bark be less likely to split. A small nail was used to hold the scion rigidly in place, as for inverted L grafting. The grafting wax was the same as that used for apples.

The length of scion used always carried seven buds. The scion wood of all varieties was obtained from trade sources, and was kept heeled in out-of-doors in the shade. At the time of grafting, the scions of Monarch and Victoria were rather drier than those of the five other varieties.

Records.

During the winter 1938-39 the number of living scions on each tree was counted and the growth of each measured. This was the only detailed growth measurement possible, but some indication of the relative vigour of whole trees could be obtained from the measurements of trunk girth, which have been recorded annually both before and since the trees were grafted. On June 28th and 29th, 1938, a very heavy gale was experienced, and considerable damage to the scions occurred. The numbers and position of the scions broken off by the gale were noted when the measurements were made.

There was very little Silver Leaf disease (*Stereum purpureum*) on the trees in 1938, but in the following season about 11 per cent. of the scions had to be removed owing to attack. As this disease may be a very important factor in the frameworking of plums, detailed records were made of its incidence and also of the size of the wounds made when the trees were prepared for grafting.

The fruit buds on all the trees in the spring of 1939 and the few fruits which were harvested in that year were counted. In 1940 there was too much blossom for a detailed count, but a visual record of its amount in relation to the size of the trees was obtained. All trees bore a crop in this season, and the weights of fruit, together with the average number of plums to the pound at each picking on every tree, were recorded.

Results.

(*a*) *Take of scions.*

Table I summarizes the take of scions, the subsequent losses from the gale of June 1938, and from Silver Leaf and other causes, as well as the numbers of

scions surviving in 1940 for cleft and bark grafts of each of the seven varieties. In each instance there were originally 120 grafts, 60 on each of two trees.

The most striking difference in take was between the cleft and the bark grafts. In general the take of the cleft grafts was good, averaging 79 per cent., but in only two varieties was the take of the bark grafts higher than 50 per cent., the average for all varieties being only 38 per cent. Of the seven varieties used, Cambridge Gage gave the best take, and takes of Warwickshire Drooper, Oullins Golden Gage and Ontario were all good, especially when cleft grafted. The two varieties Monarch and Victoria, the scion wood of which was rather dry, gave very poor takes when bark grafted, but the cleft grafts of both gave comparatively good results.

TABLE I.

Number of scions (out of 120) which took in 1938 and survived to 1940.

Variety.	Cleft grafted scions.					Bark grafted scions.				
	Take 1938.	Losses.			Survived 1940.	Take 1938.	Losses.			Survived 1940.
		Blown off.	Silver Leaf.	Other causes.			Blown off.	Silver Leaf.	Other causes.	
Cambridge Gage	113	1	0	3	109	84	5	0	1	78
Warwick Drooper ..	101	4	0	5	92	57	6	2	1	48
Ontario ..	93	5	61*	4	23	67	0	0	5	62
Oullins Golden Gage ..	100	11	0	0	89	56	4	4	9	39
Jefferson's Gage	91	5	35*	6	45	27	1	0	0	26
Victoria ..	92	17	0	1	74	23	3	0	2†	18
Monarch ..	74	1	0	21	52	6	0	2	4	0‡
Total ..	664	44	96	40	484	320	19	8	22	271
=	79%	6·6%§	14·5%§	6%§	58%	38%	5·9%§	2·5%§	6·9%§	32%

* One whole tree died of Silver Leaf.
† Only two grafts took on one tree and this tree died.
‡ Both trees died, one with Silver Leaf.
§ Percentage of those which took.

Of the two kinds of cleft graft, side grafts (83 per cent.) were slightly more successful than stub grafts (75 per cent.). This difference was significant, but the smaller difference between inverted L (41 per cent.) and awl grafts (36 per cent.) was not.

Table I also shows the numbers of scions lost as the result of the gale in June 1938. Out of 664 successful cleft grafts, 44 scions (6·6 per cent.), and out of 320 successful bark grafts, 19 (5·9 per cent.), were broken out. There was thus little difference between the two methods.

Observations at the time of the damage indicated that the exposure of the tree, the vigour of the variety and the position of the scion were the three chief causes of loss. In fact, the effect might best be regarded as being the result of a combination of the three causes. When a tree was exposed to the force of the gale and the scion growth was vigorous, the most exposed (i.e. usually the topmost) scions were broken out. As the scions inserted on the ends of scaffold branches were always either stub or inverted L grafted, these suffered most (Table II). Fourteen of the stub grafted scions blown away, for example, were from limb-end grafts ; but as some of these were not true stub grafts (owing to the lack of a suitable stub) the method cannot be regarded as making a weaker union.

It was observed that varieties with large leaves but relatively slender shoots, such as Victoria, suffered the greatest losses. However, Warwickshire Drooper

TABLE II.

Number of scions which grew successfully for each method, and the number and percentage blown off.

	Cleft grafts.		Bark grafts.	
	Stub.	Side.	Inverted L.	Awl.
Number of scions which grew ..	314	350	171	150
Number of scions blown off ..	26	18	14	5
% scions blown off	8·3	5·1	8·2	3·3

and Oullins Golden Gage, varieties with sturdy growth as well as exceptionally large leaves, also lost several scions. The longer and more numerous the scion shoots, the more top-heavy the grafted branch became, and the force of the wind was thus assisted by the exuberant growth of the scion itself. It is an important fact that the great majority of the missing scions of all varieties were broken off at or just above the graft union with a jagged, tearing break, and were heavily and healthily callused. There is thus no suggestion that any of the seven varieties were incompatible with the Czar intermediate.

After the damage from the 1938 gale had been assessed, two series of Ontario scions were selected from frameworked plum trees not included in this experiment. These were treated by (1) pruning away one-half of the length of the shoots, and (2) preventing the spreading habit of the shoots by encircling them with rubber bands. As no further gale damage has taken place on any of the trees during the three years since grafting, there has not been any opportunity to test the success of these preventive measures.

(*b*) *Silver Leaf disease.*

Returning to Table I, the losses from Silver Leaf up to the summer of 1940 are shown in columns 4 and 9. Very little disease was observed in 1938, only about 1 per cent. of the living scions being affected. In the following season, however, a more serious attack was recorded. During 1939 and 1940, 14·5 per cent. of the cleft grafted and 2·5 per cent. of the bark grafted scions were lost from this cause. This large difference is not so much due to the number of trees affected as to the greater severity of the disease on the cleft grafted trees. Of the three infected, one whole tree of Jefferson's Gage and one of Ontario died, accounting for 78 scions, while nearly half of the second tree cleft grafted with Ontario became affected.

A careful examination of the wounds made in preparing the trees for grafting showed that, although the number of them on the cleft grafted trees was not greater than on the others, the three badly infected trees did have an unusually large number of large wounds over 2 inches in diameter.

It may also be noted that the cleft grafting was done about a fortnight earlier than the bark grafting. Both operations took place during the period in which wounds are known to become more easily infected by the Silver Leaf fungus than later in the spring and early summer; in this early period it is not now considered advisable to prune plum trees. It is possible, however, that the earlier grafts were more vulnerable and this may have contributed to their more serious infection. In deciding on the time at which to graft, therefore, this point should be borne in mind, and it may be advisable to graft plum trees later than was done in this experiment. It has been shown that apples can be both cleft and bark grafted successfully as late as June, and there seems no reason why this should not be so for plums also, except that plum scion wood appears to be more difficult to store successfully.

(*c*) *Other losses.*

Columns 5 and 10 of Table I show that there were quite a number of losses not accounted for either by the gale or by Silver Leaf. They were distributed fairly evenly over the seven varieties and were proportionately about the same for cleft and bark grafts. The only outstanding variety was Monarch, in which there was rather a large number of such losses on the cleft grafted trees. Some of the dead scions occurred in the centre of the trees and were probably due to competition and shading by the more vigorously growing scions higher up the branch and on the outside of the tree. It is thus probably better to avoid placing scions in positions in the centre of the tree.

There was no evidence of incompatibility in any variety.

Table I shows finally the number of scions surviving in 1940. In spite of the greater losses from Silver Leaf, the cleft grafted scions were still definitely

superior, 58 per cent. of the original scions grafted two years earlier being alive as against 32 per cent. of the bark grafted ones..

(*d*) *Wood growth.*

Although initially equal numbers of scions were inserted in each tree, the wide differences in take and the subsequent casualties were the cause of a very high variation in the growth and cropping of the trees. It is difficult, therefore, to disentangle the differences between the varieties and methods of grafting from those consequent on the success or failure of the original grafts.

TABLE III.

Mean wood growth in metres for two grafting methods and seven varieties on Czar intermediates.

Variety.	Cleft.	Bark.	Mean.
Warwickshire Drooper ..	72·6	36·7	54·7
Cambridge Gage	60·2	42·8	51·5
Oullins Golden Gage ..	47·7	20·0	33·9
Ontario	42·4	16·2	29·3
Jefferson's Gage	40·3	9·0	24·6
Victoria	34·4	7·9	21·2
Monarch	18·4	0·6	9·5
Mean	45·1	19·0	

Table III shows the total wood growth per tree in 1938. In this no allowance is made for the variable take, and most of the differences shown are evidently dependent on the number of scions on the trees (see Table I). There was a large difference between the cleft and the bark grafts. This, however, was very nearly proportional to the number of scions present on each. It cannot be said, therefore, that scion growth from the cleft grafts was more vigorous than that from the bark grafts in the first season.

In the last column of the Table, varieties showing non-significant differences are bracketed together. Here again, high variation renders the detection of differences difficult, and those shown are largely due to the varying takes. However, there is some evidence that Warwickshire Drooper and Cambridge Gage scions really made more growth than the others. There was very little difference in growth between stub and side grafted scions or between inverted L and awl grafted ones. It was not possible to continue measurements of growth after the first season, but observations have indicated that, in some instances, more growth per scion was made where there were fewer scions alive on the trees. Nevertheless the initial take of scions and the subsequent losses have remained the main influences on the growth of the trees.

(*e*) *Fruit buds in* 1939.

High variation again made confirmation of the smaller differences in fruit bud formation difficult. Nevertheless there were large differences in the number of fruit buds borne in 1939, as shown in Table IV. The units are averages of two trees and the means of variety and method are included.

TABLE IV.

Number of fruit buds in 1939 *and mean number of scions living, for each method. Seven plum varieties on Czar intermediate.*

Variety.	Method of grafting.				
	Stub.	Side.	Inverted L.	Awl.	Mean.
Oullins Golden Gage ..	16·5	13·5	29·0	18·5	19·4
Ontario	152·0	175·5	57·5	61·0	115·5
Jefferson's Gage	32·5	60·5	14·0	10·5	29·4
Cambridge Gage	23·5	24·5	22·5	19·5	22·4
Warwickshire Drooper ..	209·5	369·5	95·0	89·5	190·9
Monarch	94·5	150·0	0	0	61·1
Victoria	131·5	216·5	33·5	43·5	106·1
Mean No. fruit buds ..	94·3	144·3	33·9	33·8	77·1
Mean No. living scions (out of 60)	41·1	47·1	22·0	20·6	32·7

Obviously the scions inserted by cleft grafting methods (stub and side) produced more fruit buds than those by bark grafting methods (inverted L and awl), even allowing for the greater number of scions which grew successfully on cleft grafted trees. The side grafted scions carried more fruit buds per scion than the stub grafted ones, and the three most prolific varieties were Warwickshire Drooper, Ontario and Victoria. There seemed to be no correlation between vigour and blossoming. The vigorous Warwickshire Drooper, for instance, produced by far the greatest quantity of blossom, whereas Cambridge Gage, which also showed much vigour, had a relatively small number of fruit buds.

(*f*) *Crops in* 1939 *and* 1940.

The only two varieties to bear appreciable crops in 1939 were Warwickshire Drooper and Victoria. Three out of the four trees of the former variety bore over 60 fruits, while rather less than half the number were harvested from the latter.

In 1940 all varieties blossomed profusely. That season was an excellent one for plums generally and all the varieties in this trial cropped well. In

Table V the actual crops harvested in units of two trees, except where stated, are summarized.

Evidently, since there were many more living scions, as shown in columns 2 and 5, the crops from the cleft grafted trees bulked much more fruit than those from the bark grafted trees. After eliminating the effect of the variable number of scions, however, the difference is greatly reduced and is probably non-significant. Of the seven varieties, Warwickshire Drooper was again outstanding, producing double the crop of all other varieties. Comparison of the cropping of Ontario, Oullins Golden Gage, Jefferson's Gage and Cambridge Gage is so complicated by the variation in number of scions that it is difficult

TABLE V.

Comparative cropping of the seven varieties framework grafted by cleft and bark methods in the third season after grafting.

Variety.	Cleft.			Bark.		
	Number of scions on two trees.	Total crop. lb.	Crop per 100 scions. lb.	Number of scions on two trees.	Total crop lb.	Crop per 100 scions. lb.
Cambridge Gage	109	124·1	115·1	78	85·1	114·5
Warwickshire Drooper ..	92	306·6	338·1	48	220·1	455·3
Ontario	23*	58·4	177·0	62	58·3	92·9
Oullins Golden Gage ..	89	135·0	155·0	39	44·2	96·6
Jefferson's Gage	45*	67·0	148·9	26	36·0	155·2
Victoria	74	152·8	206·2	18*	28·1	156·1
Monarch	52	113·2	216·1	No trees		

* One tree only.

to tell whether there was any significant difference or not. In crop per 100 scions, Cambridge Gage appears inferior ; but, by the third season, some of the trees with few scions had made considerably more growth per scion than those, such as Cambridge Gage, in which there was a high survival, and this may account for their apparent superiority in cropping. Victoria and Monarch both cropped well as far as the casualties allowed.

TESTING COMPATIBILITY BY MEANS OF FRAMEWORKED GRAFTING.

The literature on rootstock/scion incompatibility in stone fruits was reviewed in detail by Argles (1937). He pointed out that in plums almost all known forms of incompatibility, from the complete failure of bud unions to the production of short-lived or weak growing trees, are represented. Interspecific

and intervarietal incompatibilities occur in all plum growing countries. Amos and others (1936) showed that Czar and President varieties are incompatible with several rootstocks in common use (notably Common Plum), but that Victoria and Purple Egg rarely show this phenomenon. These workers also showed that with incompatible plum combinations either the buds failed completely to take, or death of the trees might take place in the nursery or at any age up to several years in the orchard.

Heppner and MacCallum (1927) conducted topworking trials in California which again showed several instances of rootstock/scion incompatibility. They noted, however, that reciprocal combinations did not always show the same effect.

If the frameworking of plums is to become a common practice, the inter-compatibility of the new varieties and the frame intermediates is a matter of vital importance. If, for example, a variety such as Czar, already known to be incompatible with certain rootstocks, were further found to be uncongenial to many commercial varieties likely to be worked upon it, the value of the method would be seriously limited.

An investigation was, therefore, started to study the behaviour of a wide range of high quality and of late ripening varieties when frameworked on mature trees of three varieties available for the purpose. The method had the further advantage of economy of material and effort, in that several varieties could be worked on individual branches of the same tree.

Material and methods.

Twenty-two 13-year-old trees were selected from the same plantation as that described in the first part of this paper. These were of three varieties: (1) Czar, on Damas C, Myrobolan and Pershore rootstocks. (2) Purple Egg, on Myrobolan, Marianna and Common Mussel. (3) Utility, on Common Plum and Marianna. Eight trees each of Czar and Purple Egg and six of Utility were framework grafted during the second week in April 1938. Twenty-four varieties were grafted on Czar (including Czar itself) and twenty-three each on Purple Egg and Utility trees. Six varieties (ten scions of each) were grafted on each Czar and Purple Egg tree, but as the Utility trees were larger, the same number of scions of eight varieties were grafted on each tree. Two replications of each combination were used.

Cleft grafting methods only (stub and side) were used, the number of scions inserted by each method depending largely on the number of suitably placed stubs that were available.

The varieties used, in order of crop maturity, were:

*Early Laxton.	Jefferson's Gage.
*Czar (on Czar intermediate only).	Giant Prune.
Ontario.	Warwickshire Drooper.
Oullins Golden Gage.	Bryanston Gage.
Laxton's Gage.	Late Transparent.
*Belle de Louvain.	Reine Claude de Bavay.
Cambridge Gage.	*Late Orange.
*Victoria.	Old Transparent.
Old Green Gage.	*Golden Transparent.
*Denniston's Superb.	*Coe's Golden Drop.
*Cox's Emperor.	*Monarch.
*Comte d'Althan's Gage.	*President.

The majority of these are of a high dessert quality, and they were selected with a view to finding regular cropping sorts suitable for commercial purposes. Certain well-known mid-season varieties are included, the remainder being late varieties, not necessarily of high quality, but of commercial value because of their season.

The scion wood was obtained chiefly from trade sources and was kept heeled in out-of-doors in the shade. At the time of grafting, twelve of the twenty-four varieties were noted to have comparatively dry scion wood, and these are indicated with an asterisk in the list above. The scion wood of Czar was particularly dry. Scion wood could not be obtained from the Czar trees which were being frameworked, since they were in fruiting condition and had no matured vegetative shoots suitable for scions. This variety was grafted only on itself.

In a subsidiary experiment, twenty varieties were budded on four trees of Czar. Experience in Germany had led to the belief that Czar was a difficult variety to graft, and that budding gave better results. The trees were cut back in the spring to provide young vigorous growth for budding in early August, but insufficient new wood was produced and some of the buds had to be inserted in old wood. The latter were practically a complete failure and in general the take of buds was very low (32 per cent.). This made any comparison of compatibility very difficult, and no further reference to this trial will be made in this paper.

Records.

The main records were the same as those described in the previous section of this paper. They included take of scions, subsequent losses from the gale

* Scion wood noted as dry at time of grafting.

of June 28th, 1938, and from Silver Leaf, an estimate of growth in the first season, fruit bud formation and yield up to the end of 1940. In addition, a careful look out was kept for any evidence of incompatibility, as shown by the characteristics of the growth and foliage.

Results.

(a) *Take of scions.*

Table VI summarizes the take of scions of twenty-three varieties on the three intermediates, the subsequent losses from gale damage, Silver Leaf and other causes, and the survival in 1940. The variety Czar is omitted, as it was grafted only on Czar intermediate and every graft failed to grow, probably owing to the poor condition of the scion wood. It will be seen that on none of the intermediates was the general take high, varying from 214 (46·5 per cent.) on Utility to 281 (61·1 per cent.) on Czar. The differences were somewhat reduced by the end of the season as a result of the June gale, there being a considerably lower proportion lost on Utility than on the other two intermediates.

Table VI.

Number of scions which took (1938) *and survived* (1940) *out of twenty-three varieties on three intermediates.*

On	Number of scions inserted.	Take 1938.	Losses.			Survived 1940.
			Blown off.	Silver Leaf.	Other causes.	
Utility	460	214	23	33	20	138
Purple Egg ..	460	238	54	9	16	159
Czar	460	281	40	40	44	157
	1,380	733	117	82	80	454

There was great variation in the take of different varieties on all intermediates, from Cambridge Gage, all of the scions of which grew, to Monarch, which achieved only a 13 per cent. success. There was only one instance of complete failure to grow besides Czar on Czar, viz. Denniston's Superb on Purple Egg. Only two scions of Cox's Emperor on Utility and of Monarch on Czar grew, and in each case both died subsequently for no clear reason. The take of Late Orange was also very low on all intermediates. As, however, all these varieties were among those noted as having rather dry scion wood, it cannot be said with any certainty that these combinations were incompatible. Indeed, of the twelve varieties previously noted as having dry scions, all had less than 50 per cent. take, while of the twelve, the scions of which were in good condition,

only two gave less than 50 per cent. take. The following varieties had a 75 per cent., or higher, take on all intermediates :

Cambridge Gage.	Old Green Gage.
Warwickshire Drooper.	Laxton's Gage.
Ontario.	Oullins Golden Gage.

Of these, the last two suffered particularly heavily in the gale, half the scions of Laxton's Gage on Purple Egg and nearly half those of Oullins Golden Gage on Purple Egg and Czar being blown away.

(*b*) *Silver Leaf disease.*

Again there was little Silver Leaf to record in 1938, but, as in the first trial, considerable infection was observed in 1939. The most striking difference in the losses from this cause was between the three intermediates ; only nine grafts (3·8 per cent.) on Purple Egg were lost, whereas nearly four times as many were affected on the other two intermediates. This difference in susceptibility of the intermediates is probably mainly responsible for any differences between the varieties worked on them. Thus, on Utility, two-thirds of the affected scions were on a single tree, on which all varieties suffered alike. Again, on Czar, two badly silvered trees accounted for 35 of the 40 affected scions. Only one scion variety, Warwickshire Drooper, seemed outstandingly susceptible, losing 40 per cent. of its scions, these being distributed over all three intermediates.

(*c*) *Other losses.*

Losses, the causes of which were undetermined, were distributed evenly over all the scion varieties, but occurred most frequently on Czar. Shading has been mentioned as one cause and, in this trial, competition between strong and weak growing varieties frameworked on the same tree would seem to be another. Also, where the majority of scions of one variety were growing strongly on one branch of a tree, a poor take on another branch would be likely to suffer. One side grafted scion of Old Transparent Gage broke away from its Czar intermediate in the summer of 1940. The branch was then apparently growing normally with healthy foliage ; but the break was a clean one and showed all the evidence of delayed incompatibility. Up to the time of writing (July 1941) no further breakage has taken place, but the compatibility of this combination must definitely be regarded with suspicion. In no instance were the unexplained losses large enough in themselves to warrant any suspicion of incompatibility.

The numbers of scions surviving in 1940 are given in the last column of Table VI. The initial advantage of Czar over Purple Egg had by that time been lost, but the numbers alive on Utility were still behind those on the other two intermediates.

(*d*) *Wood growth.*

The total growth made in 1938 by the scions remaining after the severe gale in June of all variety-intermediate combinations, is illustrated in Fig. 1. The amount of wood growth is indicated as follows:

0-20 metres	..	White squares.
21-40 ,,	..	Single shaded squares.
41-60 ,,	..	Double ,, ,,
61-80 ,,	..	Black squares.

The difference between any two intermediates is not large, but is in favour of Purple Egg. This, it should be noticed, is in spite of a lower take than Czar.

The scion varieties which produced most wood growth were Cambridge Gage, Warwickshire Drooper, Old Green Gage, and Ontario, all of which also had a high percentage of scions alive at the end of the season. The remaining varieties are well below these four, but their range was very wide, some varieties, such as Golden Transparent on Czar and Cox's Emperor on Czar and on Utility, making very little growth on the few scions which did unite successfully. Jefferson's Gage and Victoria on Czar had a relatively small number of scions which grew, but these produced excellent growth.

Those varieties which produced most growth cannot on that account be called the most vigorous. The large total growth was caused chiefly by the larger number of scions which united well. However, on the whole, those varieties making most growth were also among the most vigorous.

(*e*) *Fruit buds in* 1939.

The numbers of fruit buds in the spring of 1939 are also represented in Fig. 1 on the following multiple scale:

0 to 20 fruit buds	..	White squares.
20 to 60 ,, ,,	..	Single shaded squares.
60 to 140 ,, ,,	..	Double ,, ,,
140 to 300 ,, ,,	..	Black squares.

It will be noted that the scions which appeared to be rather dry at the time of grafting and gave poor takes were among the lowest in total growth and, except for Victoria, were also among those with the least number of fruit buds. The three varieties which bore most fruit buds were Warwickshire Drooper, Giant Prune and Laxton's Gage. The first named variety is the only one of the three which also made a relatively large amount of growth. Czar and Utility intermediates had more fruit buds with all varieties than Purple Egg. There was a negligible amount of fruit on all varieties in this season.

(f) Fruit buds and fruit in 1940.

All varieties blossomed in 1940. It was not possible to make actual counts in that season, but a record was made by eye of the relative blossoming of all varieties irrespective of the number of scions present. On the whole those on Czar blossomed most heavily and those on Purple Egg least. Of the scion varieties, Warwickshire Drooper, Cambridge Gage, Laxton's Gage, Giant Prune

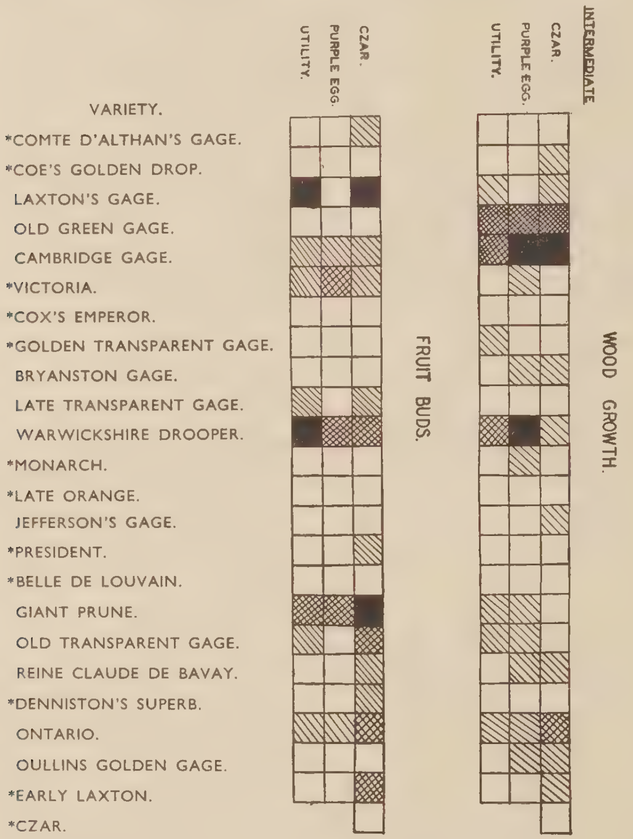

FIG. 1. Diagram illustrating wood growth and number of fruit buds in 24 plum varieties on 3 intermediates. * Scion wood noted dry.

and Early Laxton blossomed heavily, while Coe's Golden Drop, Bryanston Gage and Reine Claude de Bavay were also good.

The plum season was a good one and only two varieties, Cox's Emperor and Late Transparent, failed to set any fruit. The actual weights of fruit were largely dependent on the number of scions remaining on the trees, and, therefore, gave little reliable information as to the relative cropping merits of the varieties.

The four varieties with the largest total crops were Giant Prune, Ontario, Cambridge Gage and Warwickshire Drooper, the first named yielding 147 pounds from twenty-eight scions on the six trees. However, a better idea is obtained if the crops per scion are compared for varieties having approximately the same number of scions surviving. In the following Table the varieties are classified according to the number of scions in 1940 and size of crop per scion.

TABLE VII.

Comparative cropping per scion of twenty-three scion varieties on all intermediates in 1940.

Percentage scions surviving.	Size of Crop. Heavy (Over 2 lb.)	Medium (1-2 lb.).	Light (Under 1 lb.).
Over 75	—	Cambridge Gage	—
50-75	Ontario	—	Old Green Gage Old Transparent
25-50	Giant Prune Warwickshire Drooper Belle de Louvain* Victoria*	Bryanston Gage Oullins Golden Gage	Coe's Golden Drop* Reine Claude de Bavay Laxton's Gage Late Transparent
Under 25 ..	Early Laxton*	Comte d'Althan's* Denniston's Superb* Jefferson's Gage	Late Orange* Monarch* Golden Transparent* President* Cox's Emperor*

* Dry scions.

Among the heavy cropping varieties Giant Prune and Warwickshire Drooper were outstanding. Both are mid-season to late maturing varieties and have already proved their high yielding potentialities in commerce. Neither Early Laxton nor Ontario are of very high quality, but they compare favourably with other plums in the early part of the season. The latter had in take, growth and crop, the best record for all the less well-known varieties in this trial. Early Laxton was handicapped at the start by the condition of its scion wood and is evidently worth further attention. Cambridge Gage had the best record for the high quality sorts, but largely by reason of the high proportion of successful grafts and its strong growth. Bryanston Gage and Oullins Golden Gage did fairly well. Despite profuse blossoming, Laxton's Gage did not crop well. Those varieties which had under 25 per cent. survival can hardly be said to have had a fair chance, since all but one had dry scions originally. Among the

poorest were the late maturing varieties, Monarch and President, both known to be slow to crop in normal circumstances.

(g) *Foliage.*

During the three seasons after grafting, there was little evidence of incompatibility in the characteristics of growth and foliage. The only variety that excited suspicion was Late Transparent, the leaves of which were upcurled and of pale colour each year. Furthermore this variety, the scions of which were in good condition, had a rather poor take, was among the poorest in growth and produced little blossom and no fruit. Nevertheless this occurred on all intermediates in this trial, and the same foliage symptoms were found on trees in the nursery budded on a wide range of rootstocks. It seems probable, therefore, that these are characteristics of the variety and are not due to incompatibility.

DISCUSSION.

Although these experiments have shown that the framework grafting of mature plum trees is a practical proposition, the operation evidently requires greater care than with apples. In preparing the scaffold variety for grafting, large wounds must be avoided, especially on varieties known to be susceptible to Silver Leaf. The scion wood must be in first class condition, since if it becomes at all dry poor takes must be expected. Cleft grafting is superior to bark grafting, and it seems desirable that the operation should be carried out as late in the season as possible, when the trees are less vulnerable to Silver Leaf. Stub and side grafts are apparently equally good. When once the scions have started growth, some form of summer pruning is probably desirable, especially in exposed situations and for strong growing varieties.

Twenty-three varieties frameworked upon three intermediates gave little evidence of incompatibility in the first three seasons after grafting. Nevertheless it is still possible that delayed incompatibility may show itself, and it would be inadvisable to carry out frameworking of one variety on another on a large scale without a previous trial on a small one. It is, however, encouraging to find so little evidence of incompatibility with a variety such as Czar, itself rather particular about the rootstocks on which it will grow.

SUMMARY.

Two experiments designed to explore the possibilities of frameworking mature plum trees are described. In the first, cleft and bark grafting methods were compared, seven scion varieties being grafted on 14-year-old Czar trees. Cleft methods, stub and side grafts being equally good, proved superior to bark grafts (inverted L and awl) in take. They lost, however, a rather higher percentage of scions from Silver Leaf, though this was probably a mischance, a few

badly affected trees being found to have rather larger wounds, made in preparing the trees for grafting, than the others. Severe damage to scions in the first season from a summer gale indicated the need for some form of summer pruning, especially for vigorous varieties. There were large differences in the growth and cropping of the seven scion varieties, but these were complicated by a big variation in take ; for this, the condition of the scion wood was of great importance.

In the second experiment, the intercompatibility of twenty-three scion varieties, including high quality and late maturing sorts, and three intermediates, was tested. Six to eight varieties were cleft grafted on individual scaffold branches of each tree. The factors mentioned above again complicated the results, differences in susceptibility of the intermediates to Silver Leaf being clearly shown. However, up to three years after grafting, there was no clear evidence that any of the sixty-nine combinations tried were incompatible, despite the fact that one of the intermediates and some of the scion varieties were known not to be compatible when worked on certain rootstocks.

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STUDIES IN FRAMEWORK GRAFTING OF MATURE FRUIT TREES

IV. A COMPARISON OF FRAMEWORKED AND TOPWORKED APPLE TREES

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There are two main ways in which fruit trees may be changed from one scion variety to another—by frameworking and by topworking. Both methods have been described in considerable detail (Garner and Walker, 1938; Anon., 1938) but no direct comparison of frameworked and topworked trees appears to have been made. From 1932 onwards methods of reworking fruit trees had been under investigation at East Malling, and in September 1934 it was suggested that a trial of some of the more usual methods of reworking should be undertaken. Fruit growers had frequently experienced difficulty in successfully reworking certain varieties which contracted Silver Leaf disease (*Stereum purpureum*) soon after grafting. When the Newton Wonder apple was topworked with another variety it quite frequently succumbed to this disease. Many growers wished to change from Newton Wonder to other varieties; it was therefore of some importance to discover safer methods of reworking.

There were really two problems, one of grafting method and the other of satisfactory varieties. There was insufficient material to permit the testing of a number of varieties, and it was decided to confine the trial to one of method on trees of Newton Wonder, using the single variety Laxton's Superb for the new scion.

Material.

Eighty thirteen-year-old standard Newton Wonder trees were available. They had originally been worked at ground level in the nursery on the clonal rootstocks Malling I, X, XII, XIII, XV, XVI, A, F, C, and H and on Long Ashton G8. Sixty-four of them on eight of the Malling rootstocks were set aside for the trial, the other sixteen being used for practice in grafting methods so that the operators might have some experience of them before the trial began. At the beginning of the trial the trunks of the trees varied in girth from 32·8 cm. to 44·5 cm., and the over-all height and spread of the trees was some $5\frac{1}{2}$ metres and 5 metres respectively.

The trees were 30 feet apart, in alternate rows with the variety Allington Pippin of the same age. Bush trees of Lane's Prince Albert and standard pear trees were interplanted at 15 feet. The sixty-four trees in the trial were spaced equally in eight rows.

The Laxton's Superb scion wood was obtained from a grower at Tenterden, in Kent, during the winter of 1934-35. The sealing material for all grafts was a home-made hot brush wax of proved efficacy (Garner and Walker, 1938).

LAYOUT.

There were four treatments :

R. Rind grafting.

O. Oblique cleft grafting.

RB. Rind grafting with retention of branches.

S. Frameworking (Stub grafting method).

Each treatment occurred twice in each row of trees and twice on each of the eight original stock/scion combinations.

METHODS.

The methods R (rind), O (oblique cleft), and RB (rind with branches) are all topworking ones in which the head of the tree is removed and re-formed by the growth of the new scions. The method S (stub graft) is a frameworking one in which the main framework branches are retained and scions are inserted at intervals of about 10 inches along each branch. One ungrafted and three newly grafted trees are shown in Figs. 3-6, Plates I and II. Some 150 scions were used in each frameworked tree (S), as compared with from eight to fourteen, according to the nature of the branch system, on each tree grafted by the other three methods (R, O and RB). The trees were prepared at the time of grafting, which was begun and completed between March 27th and April 16th, 1935. It was considered that the Newton Wonder trees possessed more than sufficient branches, hence crowding ones were sawn out at their base, this being necessary for all the trees. The comparatively large wounds caused by branch removal were sealed immediately with hot wax as used throughout the grafting.

In the topworking methods the main limbs were cut transversely at from 15 to 20 inches from the crutch of the tree. The smaller limbs received one scion and the larger two. An average of twelve scions was placed on the R and O trees and from eight to ten on the RB trees. These last received more scions in the following year as will be described later. All the scions bore three buds only.

Both rind and oblique cleft grafts have already been described in some

detail (Baltet, 1910 ; Anon., 1938). The method of rind grafting used was that normally practised. In it the scion is inserted beneath the rind of the stock and tied in position. Soft string (fillis) was used for tying. In the oblique cleft graft the limb is cleft half-way along chords of the transverse section. The scions inserted in the clefts need no tying. Limbs receiving one scion only were cleft radially. The RB method was the rind method with the retention of two main branches, colloquially known as sap-drawers. The retention of such limbs is considered to assist in the recovery of the tree from the shock caused by the removal of the main branches. The sap-drawer branches in the trial were selected on opposite sides of the tree, as low as possible. Side branches were chosen because central branches might dominate the growth of the scions beneath them and would be difficult to remove later without damage to the new scions. One branch only at one side might encourage a one-sided development. The sap-drawer branches were cut back transversely one year later, as in the first original topworking, and rind grafted.

All the small growths on the limbs below the grafts were left intact in all the topworked trees. The frameworked trees, treatment S, were stub grafted with an average of 153 scions per tree. The stub graft method of frameworking was developed at East Malling Research Station (Garner, 1934) and has already been described in detail (Garner and Walker, 1938). In 1935 the long scion used in frameworking had not become an established practice (Hilton, 1942) and it was decided to use three-bud scions. The ends of the branches were cut back to a stub grafted lateral, where the branches were a little over an inch in diameter. The tallest branches were shortened rather more severely and some of the wounds so made were 2 inches in diameter. It is now realized that such drastic cutting back was inadvisable both for apples and plums (Hilton and Hoblyn, 1942), especially in varieties susceptible to diseases such as Silver Leaf, which are contracted through wounds. Further, it may be of some importance to record that, in tall trees, wounds at the apex of upright branches facing the sky are liable to be missed when applying grafting wax. No scions were placed within 18 inches of the crutch of the tree.

A record was kept of the time taken to prepare and to graft each tree. The topworked trees were completed in $1\frac{1}{2}$ man hours, including removal of branches, complete grafting and sealing of the grafts. The total time spent on the frameworked trees was 12 man hours. Experience of similar work since then has shown that the time taken was somewhat excessive. Even so, the times are probably comparative, and it may be said that the frameworking operation occupied the same number of workers eight times as long as the topworking one. Against this it must be remembered that, as will be seen, frameworked trees return to full cropping capacity more quickly and are less liable than ordinary topworked trees to succumb to Silver Leaf disease.

SURVIVAL.

(*a*) *Breakage.* By the end of the season in which the grafting was done the topworked trees differed in the numbers of surviving scions. None of the scion growth was supported in any way, as it was hoped to discover the tenacity of scions worked by the various methods. No breakages occurred on the frameworked trees. Of the topworking methods the oblique cleft grafts showed least loss by breakage, only 1 per cent. being wholly broken out (see Table I). Of the rind grafted trees, those with sap-drawers (RB) lost 7 per cent. of scions by breakage, as against 21 per cent. lost by the trees without sap-drawers (R), and in number of surviving scions they were very little inferior to the oblique cleft grafted trees.

TABLE I.

Condition of scions at the end of the first season after grafting. (Per 100 scions inserted.)

Method.	Undamaged.	Scions which failed to grow.	Partly broken.	Wholly broken.	Total dead and broken.
R	65	12	2	21	35
RB	84	8	1	7	16
O	88	7	4	1	12

(*b*) *Disease.* All the Newton Wonder trees were apparently quite healthy when the grafting was done in the spring of 1935. In September of the same year four trees had cankers. For example, in a topworked tree three cankers, each an inch wide, extended 1 foot in length on each of two main branches. Two scions had not grown and two had made only 1 inch of growth before dying. On one of the frameworked trees a canker 1 inch wide extended for 5 feet along one of the main branches. These cankers were all of the papery bark type.

In February 1936 all the trees were surveyed and an attempt was made to estimate the number and extent of the cankers. In the topworked trees individual cankers were placed in the following classes :

1 =Cankers of 1 to 4 square inches or a 1 to 6 inch wide girdle at the apical end of the branch.

2 =Cankers covering more than 4 square inches or a girdled area 6 inches or more wide at the end of a branch.

3 =Cankers involving entire branches.

Similar categories if applied to the large system of the frameworked trees would have given a false impression of the comparative severity of the cankers, hence in recording cankers on these trees the actual length of branch involved,

in feet, was recorded for individual branches. It is realized that any estimation on these lines is open to criticism, but in this trial it did seem to give some idea of the severity of the cankering in trees treated in different ways. Difficulties which arose were the variation in the number of branches grafted and the method of recording branches in frameworked trees. The total numbers of branches and the number of these showing cankers is set out in Table II. It will be seen that cankers were more numerous on topworked than on frameworked branches, and of the topworked trees the rind grafted ones were most severely affected ; but the retention of ungrafted branches had a very beneficial effect in reducing the percentage of affected branches from 65 to 26. In the spring of 1936 all Newton Wonder shoots were removed from the crutches and main stems of the trees, except where severe cankers had occurred, in which event such shoots were left to encourage growth and healing.

TABLE II.

Cankers at the end of the first year.

Treatment.	No. of branches grafted.	No. of cankered branches.	% of branches cankered.	Total canker estimate. (Topworked trees.)
R	153	99	65	138
RB	109	28	26	34
O	161	12	7	20
S	284	12	4	—

Where scions had died on healthy limbs these limbs were cut back and regrafted. Severely cankered portions were cut away and the wounds dressed with a bituminous tree seal. A few of the cankered branches removed were examined in the field and in the pathological laboratory by Dr. Wormald. Although no fungal fructifications were present on these trees at the time, cultural tests and inoculation experiments showed that they actually contained mycelium of the Silver Leaf fungus (*Stereum purpureum*). In May 1936 it was noticed that cankers had apparently ceased to extend and that a healthy callus was forming at their margins.

In July 1936 the trees were surveyed again and a record was taken of the presence of silvered foliage. The numbers of healthy trees showing no silvered leaves in each treatment, out of sixteen, were as follows : Methods RB and S twelve each, method O eight, and method R seven. At this time two of the rind grafted trees, both on rootstock Malling No. XII, were so severely affected that it was decided to grub them. By the end of 1936, two seasons after grafting, eleven trees were removed because of severe cankering. In 1937 a further five trees were removed, in 1938 two more, and one at the end of 1939.

The effect of grafting method on the survival of trees is shown in Table III. Since the end of 1939 it has not been necessary to grub any trees, and a survey made in September 1941 revealed no Silver Leaf.

Of the trees on different rootstocks, those on the more vigorous varieties appeared to succumb more readily than the others. There were eight trees on

TABLE III.

Losses from Papery Bark Canker in seven years after grafting.

	Number of trees grafted.	1936.	1937.	1938.	1939.	Survived 1941.
R	16	5	3	1	0	7
RB	16	1	1	1	0	13
O	16	2	1	0	1	12
S	16	3	0	0	0	13

each of the eight stocks. Six of the eight on the very vigorous No. XII had to be removed, three each on Crab F and Crab A, two each on Malling No. XVI and No. XIII, and one each on Malling Nos. I, X and XV.

GROWTH.

(*a*) *New shoot growth.* Measurements were made of new shoot growth of the scions in the first three years after grafting, and these are summarized in Table IV. Since 1937 no record of length of wood growth has been made.

TABLE IV.

Mean wood growth in metres per tree of Laxton's Superb scions on Newton Wonder (on eight rootstocks) in the first three years' growth after grafting.

Method.	1935.	1936.	1937.	Total.
R	8	45	111	164
RB	12	80	164	256
O	41	150	143	334
S*	99	103	132	334

* Wood growth removed in pruning not included in growth in 1935 and 1936.

The frameworked trees made most growth in the first year, but the total growth of the oblique cleft grafted trees had equalled that of the frameworked trees by the end of the third year. The rind grafted trees made far less total growth over the three seasons. Of the topworked trees new wood growth per scion in the first season after grafting was largest in the O method, the mean growth per bud on these scions being over 4 feet. In the R and RB methods much

less growth was made, and here again the RB method did better than the R. In this trial it is quite clear that the retention of two branches as sap-drawers aided survival and growth of scions during the first season. Table IV shows that the superiority of the trees with sap-drawers over the straight rind grafted trees was maintained up to the third season after grafting, in that season the trees so treated actually making more growth than either oblique cleft grafted or frameworked trees.

(*b*) *Area of cross section of stem.* A measurement of the girth of each tree had been taken annually from planting time, and this record has been converted to area of cross section of stem as giving a more direct figure for growth. The annual increments in cross section of stem are shown in Fig. 1. The removal of

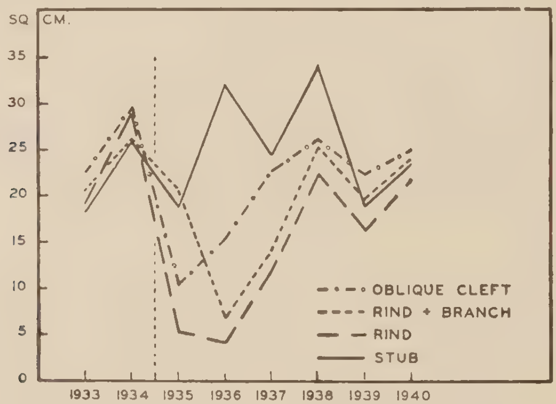

Fig. 1.

Annual increments in cross section of Newton Wonder trunks before and after reworking with Laxton's Superb. Average for trees on three rootstocks.

the head of the tree, as in the R and O methods, severely checked stem thickening in the first season. The trees worked by the O method were somewhat less checked. This was probably due to the excellent new shoot growth made by these trees. The RB and S trees were checked comparatively little in the first season. In the second season, when the sap-drawer branches were removed, the stem thickening of the RB trees was severely checked. The frameworked trees soon overcame the reduction in stem increment by rapid growth in the second year. A heavy crop of fruit in 1937 caused a falling off in the rate of stem thickening of the frameworked trees, and in 1939, when all the trees cropped, there was a similar reduction for all methods. By 1940, five years after grafting, all the trees, no matter by what method they were grafted, were once again in step.

CROPPING.

The annual crops of the trees treated by the four methods in the seven years after grafting are summarized in Table V, with the total crops for the whole period. The rapid return of the frameworked trees to cropping is strikingly shown, 150 pounds per tree having been harvested in 1937, *the third season* after grafting. In contrast, not one of the topworked trees had borne a crop of this size by 1941, seven years after grafting. The superiority of the frameworked trees was maintained in the first seven seasons, and at the end of the period they had averaged nearly three times the crop of each of the others. Of the topworked trees, the oblique cleft grafted ones cropped rather earlier and were consistently superior to the rind grafted ones. Apart from its effect on disease resistance, and thus on the number of trees surviving, the retention of sap-drawer branches had little effect on cropping, the crops per tree being little superior to those simply rind grafted.

TABLE V.

Mean Crop in pounds per tree.

Method (Treatment)	1935.	1936.	1937.	1938.	1939.	1940.	1941.	Totals.
R	nil	nil	½	13	79	46	22	160
RB	nil	nil	1¼	10	90	53	34	188
O	nil	nil	6	40	102	67	25	240
S	¼	3	150	41	273	79	146	692

With a dessert variety such as Laxton's Superb, quality of fruit has a direct effect on price. Generally speaking the smaller the crop the larger the individual fruits. Large, poorly coloured, dessert apples are not so valuable as those of medium size and good colour. The fruit on the topworked trees was larger and less well coloured than that on the frameworked ones.

To obtain some measure of fruit quality the 1937 crop was graded according to the National Mark Standards in force at that time. All the fruit from the topworked trees was placed together and graded separately from the crop from the frameworked trees. The proportion of fruits in the grades is shown diagrammatically in Fig. 2. Quality grading, as distinct from size, is mainly dependent on colour, skin blemish and shape. Half the fruit from the frameworked trees was placed in the fancy grades, whilst only a quarter of that from the topworked trees was fit for these grades. Rather more than three-quarters of the fruit from the frameworked trees was placed in the best dessert grades for size, and somewhat less than half the fruit from the topworked trees. Clearly the fruit from the frameworked trees in the early years was not only

more abundant but of better quality than that from topworked trees of the same age.

DISCUSSION.

This experiment was an attempt to make a direct comparison between topworking and frameworking.

The removal of most of the branch system of a tree before grafting, as in ordinary topworking, temporarily reduces new shoot growth and stem thickening; it causes the tree to go out of cropping for some years and lays the tree open to a grave risk of attack by Silver Leaf disease. The retention of branches for one season in newly topworked trees has to some extent lessened the severe shock to the tree (as reflected in the thickening of the trunk), encouraged a stronger shoot growth from the scions and mitigated the effect of disease. It has, however, made little difference to the subsequent cropping of the tree. This

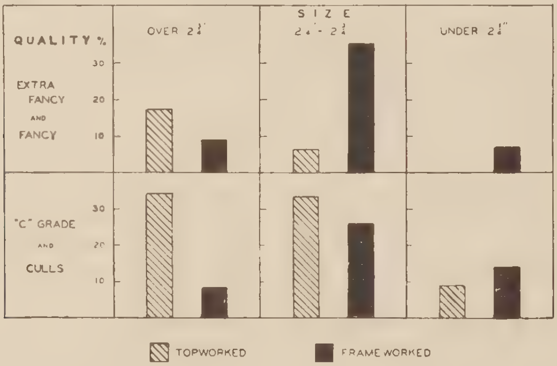

FIG. 2.

Proportion of fruit in size and quality grades. Season 1937.

may be due to the second rather severe check when the sap-drawer branches were removed in the second season, and it seems possible that if they had been removed gradually the trees would have benefited. Frameworking has conferred similar benefits and in addition has returned the trees into full cropping within three seasons.

The loss of topworked trees was not so great where growth from the new scion was abundant, as in the oblique cleft method of grafting, and it is possible only to surmise what greater benefits might have accrued had oblique cleft grafting been combined with the retention of branches.

When reworking apple trees liable to attack by Silver Leaf after grafting, it is important to retain as much of the head of the tree as possible and to avoid

making large wounds in any part of the tree. Frameworking fills these conditions.

ACKNOWLEDGMENTS.

The large amount of work involved in the collection and summarizing of the wood growth was done by Mr. R. J. Hilton, late of Macdonald College, Quebec, in the course of his studies at East Malling Research Station, and the writer gratefully acknowledges the help given by him. The writer also wishes to record his thanks to Mr. T. N. Hoblyn of the East Malling Research Station for all the help given in the summarization and presentation of these results and for much helpful criticism.

SUMMARY.

An experiment is described in the reworking of 13-year-old Newton Wonder apple trees—a variety particularly susceptible to Silver Leaf disease—with scions of Laxton's Superb.

A direct comparison was made of three topworking methods and one of frameworking. The methods of topworking used were oblique cleft grafting, rind grafting, and a further one in which the trees were rind grafted, but two whole branches of the original tree (sap-drawers) were retained for a season to facilitate recovery. On the frameworked trees stub grafting was used throughout.

Rind grafted trees (no complete branches retained) were most seriously affected by breakage and disease, made least growth (as shown in new shoot and trunk growth) and cropped less heavily than trees worked by the other methods. The retention of branches on rind grafted trees reduced loss by breakage and disease, encouraged scion growth and trunk thickening, but did not cause the trees to crop significantly more heavily than those rind grafted. Oblique cleft grafted trees lost fewer scions by breakage and disease, made more new scion growth and cropped rather more heavily than rind grafted trees.

Frameworked trees lost no scions by breakage and suffered less from disease than any of the topworked trees. New scion growth was considerably greater than in the rind grafted trees and slightly greater than in the oblique cleft grafted ones. Frameworked trees cropped heavily in the third season and continued to bear more fruit in subsequent years than trees worked by any of the other methods. The first fruits borne on frameworked trees were shown to be of better quality than those from topworked trees.

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PLATE I.

FIG. 3.
A tree before grafting.

[*Photo by J. Amos.*

FIG. 4.
A normal topworked tree.

Photographed in April 1935 at the beginning of the experiment.

PLATE II.

Fig. 5.
A topworked tree showing branches retained.

[Photo by J. Amos.

Fig. 6.
A frameworked tree.

Photographed in April 1935 at the beginning of the experiment.

WINTER INJURY TO FRUIT TREES BY FROST IN ENGLAND, 1939-40

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Introduction.

In countries where severe winter cold is normal, as in North America and N.E. Europe, injuries to fruit trees are comparatively common. According to Bradford, in correspondence with Filewicz, they occur about once in ten years in the U.S.A. and similarly in Poland, as described by Filewicz (1930).

Special kinds of winter injury, such as frost cracking, and the measures taken to prevent the spread of the injury by nailing and sealing, have been described by Overley and Overholser (1937), Potter (1938) and Gourley (1940). Macoun (1908 and 1909) found that young trees not too seriously injured by bark splitting could be saved by covering the injured parts with grafting wax. Bark injury was mentioned by Blair (1935) but no remedial measures were suggested.

In England, weather severe enough to cause winter injury to fruit trees is comparatively rare. Wallace (1929), however, recorded such damage at Long Ashton in the winter of 1928/29, and during January and February 1940 severe frosts were experienced in the South-Eastern district which caused much damage to fruit trees in some places. The present paper describes the damage that occurred at East Malling to some varieties of apple, pear and plum and the remedial measures attempted, although it is still too early to measure the full extent of the original damage and the degree of recovery. Other types of damage similar to those described by earlier writers were observed, but the effects were not so severe.

Weather conditions.

Weather conditions in December 1939 were severe, temperatures of 18° F. and 12° F. being registered in the Stevenson screen in the third and fourth weeks respectively. In January 1940 there were only three nights during which the temperature was not at or below freezing point. In the first and second weeks the night temperature fell to 17° F. and 16° F. respectively ; in the third week

* While temporarily working at East Malling Research Station.

a temperature of 2° F. was recorded on the night of 19th/20th, and it fell below 25° F. every night of that week. In the following week 9° F. was recorded on January 24th. During the first three weeks of February the temperature was at or below freezing every night except four; the lowest readings were 24° F. in the first week and 18° F. in the third.

NATURE AND EXTENT OF DAMAGE.*

Cracking and lifting of the bark from the wood of the trunk, crotch, or main branches was observed in five varieties of apple, one of pear and one of damson. Injury was also done to the one-year-old wood and to fruit- and wood-buds of pears and to the outer rind of some loganberry canes; many canes of older plants were killed outright.

Measurements were made of the length and width of the cracks and of the extent to which the bark had separated from the wood on each side of the cracks. This could best be judged by tapping with a small hammer, a hollow sound denoting the areas where the bark was loose (Filewicz, 1939; Filewicz and Modlibowska, 1940). The positions of the cracks were recorded, as was also their relationship to the position of the supporting stakes (when present) and to the tie bands. The position of the cracks with respect to the points of the compass was also noted.

Weekly measurements were made of the increase in length and width of the cracks, and of the increase in area of lifted bark on eight Cox's Orange Pippin trees. The area of initial lifting was indicated by paint, and as the injury increased, different coloured paints were successively used.

Nine days after the injury was first noted, pieces of the bark and wood were taken from several trees, near the cracks where the bark was raised. These were embedded in paraffin and microtome sections were cut and stained. Plasmolysis tests were also made with fresh material to ascertain whether the cambium was alive. Hand sections of the bark and wood were cut in April and May 1940 and in July 1941 to observe the callus formation.

Injury to pears in the form of blackened fruit buds and one-year-old wood was also studied in hand cut sections.

Damage to apples. The damage to apples, as far as could be ascertained, was confined to Cox's Orange Pippin, Duchess' Favourite, Allington Pippin, Beauty of Bath, and Lane's Prince Albert.† Nine-year-old bush Cox's Orange Pippin and Duchess' Favourite trees on Malling No. IX rootstock in the same

* The detailed figures of all recorded measurements mentioned in this paper, duly arranged and tabulated, are preserved at the East Malling Research Station and are available for inspection by any one who may wish to consult them. It is regretted that owing to unavoidable circumstances they cannot be presented fully here.—EDITORS.

† At Long Ashton in the winter of 1928-9, Wallace (1929) reported the damage as confined to Lane's Prince Albert.

plantation (the lowest at the Station) were most extensively injured. Of the 210 Cox's, 53 per cent., and of the 77 Duchess' Favourite, 30 per cent., were damaged; Beauty of Bath and Worcester Pearmain interplanted between the Cox's and Duchess' trees on the same rootstock were undamaged. The injury was in the form of longitudinal cracks down the trunks, the bark becoming separated from the wood on each side. Most of the trees had a single crack, but a fair number had two, whilst occasionally three or four cracks were present. Most of the cracks occurred on the trunks, but on a few trees they extended from the trunk to the crotch and branches; occasionally they were confined to a branch. Most of the cracks were found on the south side of the tree in which position the majority of the supporting stakes were also situated, and most of them were at or near the ties which bound the tree and stake tightly together. It will be seen later on that the damage in other sets of trees was also more frequent on the sides facing S. or S.W.

Many workers have shown that conditions on the S. side of the trunk of a tree differ greatly from those on the north. Mix (1916) states that the bark on the S.W. side is subject to wider fluctuations in temperature and to a more sudden falling of temperature when the sun sets. On a day in February he found a temperature drop under the bark on the S.W. side of 32° F. and of only 6° F. on the opposite side. Wallace (1929) supports this theory. Gardner, Bradford and Hooker (1939) observed that the day time heating on the S.W. side was further increased when snow is present, owing to the reflection of sunlight falling on the surface of the snow. Small moisture differences were shown by Müller-Thurgau (1886). Furthermore, according to Mer (1892) the maturity of the tissues and the condition of the cambium itself may vary owing to differences in the region of the tree in which cambial activity starts and finishes. All these factors contribute to make the S. side of the tree more likely to be the site of the frost crack.

As to the general cause of cracking it seems most probable that the injury results from the strain caused by the tangential contraction of the bark (due to the drop in temperature, Sorauer, 1921) often combined with the pressure exerted by the formation of an ice layer between the bark and the wood. The cracking thus depends on the physical properties of the bark itself such as thickness, elasticity and moisture content which are influenced by growth conditions and varietal resistance.

From measurements of the dimensions of the cracks made in February 1940, it was found that they varied in length from 30 to 410 mm. (mean =131) and in breadth from 1 to 9 mm. (mean =4) for Cox's, the corresponding figure for Duchess' being 35-450 mm. (mean =105) and 2 to 5 (mean =2·9). The width of lifted bark measured at the same time showed means of 12·2 mm. and 11·7 mm. on the west and east sides of the crack respectively, the corresponding

figures for Duchess' being 4·9 mm. and 9·5 mm. Thus the cracks in Cox's were wider and slightly longer and the areas of lifted bark much larger than in Duchess'.

It was noted that few trees with trunk cankers, due to *Nectria galligena*, showed any frost cracks. Possibly the lesions made by the cankers relieved some of the tension in the bark during or after the frost so that cracks were not produced.

Microscopical examination of sections of the bark and wood revealed that the cambium was either broken or had come away entirely on the lifted bark. Plasmolysis tests showed that the larger cambial cells of the medullary rays were still alive. In other cambial cells, plasmolysis was difficult to detect owing to their small size.

In another plantation, consisting of 320 11-year-old trees, 23 per cent. of Cox's Orange Pippin on four different rootstocks and 20 per cent. of Beauty of Bath on three rootstocks were found by the hammer test to have areas of lifted bark, but only a few had cracks. Trees of Cox's Orange Pippin on the very vigorous Malling No. XII rootstock were most extensively damaged, while both varieties suffered least on the dwarfing Malling IX. All the trees were staked.

Until three seasons before the damage occurred, half the trees in this plantation had been given no potash, while the other half had a moderate annual dressing of it. In the last three years the two sets had received single and double dressings of potash respectively.*

At the time when the winter injury occurred, the trees with a double potash dressing were in every way more vigorous and healthy than those with the single dressing, yet the former were the more damaged. Of the Cox's Orange Pippin on Malling Nos. IX, V and I rootstocks, practically none of the trees with the smaller amount of potash was affected, whereas from 19 per cent. to 50 per cent. of those with the larger amount were injured. Of those on No. XII the proportions damaged were one-third and two-thirds respectively. Beauty of Bath on Nos. I and V with single potash had 22 per cent. damaged and with double potash 50 per cent. ; but on No. IX none of the trees with the smaller amount of potash and only 8 per cent. of those with the larger amount were affected.

Eighty-five per cent. of the damaged Cox's Orange Pippin, and 71 per cent. of the Beauty of Bath had only one area of lifted bark per tree ; and 21 per cent. of all the damaged trees had two or more.

Out of the seventy 17-year-old half-standard trees of Allington Pippin on nine clonal rootstocks in an adjoining plantation only one, on No. XII, was

* Single potash = No potash up to 1937, 2 cwt. per acre from then onwards.
Double potash = 2 cwt. per acre up to 1937, 4 cwt. per acre from then onwards.

undamaged. There were no cracks, but large areas of lifted bark were detected. The trees were not staked.

A detailed study of the distribution of the areas of lifted bark in the sixty-nine affected trees showed that the damage was most prevalent on the south and south-west sides of the tree, although by no means confined to these positions. It occurred, roughly speaking, twice as often at the crutch as on the trunk itself, on the trunk and crotch, or on a branch.

Cracks also developed on the south side of the trunks of 14 out of 192 14-year-old bush trees of Lane's Prince Albert on clonal rootstocks interplanted with the Allington Pippins, and on one tree out of twenty-one on seedling rootstocks. Some of the bark died back on each side of these cracks.

In the same plantation neither the branches nor the trunks of Laxton's Superb, topworked and frameworked in the spring of 1935 on 17-year-old Newton Wonder, were damaged.

A 21-year-old plantation of Lane's Prince Albert on clonal rootstocks, some 50 yards away, was also affected; out of 400 trees, 184 were injured. There was no cracking of the bark but 270 areas of lifted bark, distributed mainly over the trunks and crotches, were detected. Of these, 157 were small (up to 50 sq. cm.), 109 medium sized (from 50-300 sq. cm.) and 4 were over 300 sq. cm. in area.

A comparison of the damage to these trees on eleven different Malling rootstocks showed that all of them on No. VI, but only 15 per cent. on No. IX, were affected. Between these two extremes came the trees on Nos. I, III and X (85%, 80% and 70%), then those on Nos. II, XIII, VIII and V (60%, 55%, 50% and 50%), lastly those on Nos. XII and XVI (38% and 30%). Thus, the damage was least on the least vigorous rootstock, it was considerable on the vigorous ones but most severe on the rootstocks of medium vigour.

The damage to apples described above was distributed at random and was not confined to headland trees or to particular spots within the affected plantations.

Damage to pears. Trunk cracking was observed on the south side of four trees of Conference, one a 20-year-old tree on Quince A rootstock, the three others 10-year-old trees on Quince C.

While the fruit-buds of all varieties of pear at the Station were damaged to some extent, in no instance was the injury sufficient to prevent the setting of heavy crops. On four varieties 1-year-old shoots were also affected.

In the fruit-buds the pith was blackened at the base of the bud scales. This was especially severe in Catillac, Beurré d'Amanlis and Dr. Jules Guyot. Sometimes the styles were blackened before the buds opened. This was wide-spread in Conference, Dr. Jules Guyot, Beurré d'Amanlis, Fertility and Pitmaston Duchess, but only slight in Beurré Hardy, Catillac, Hessle and

Beurré Alexandre Lucas. There was practically no injury in Emile D'Heyst, Doyenné du Comice, Durondeau and Marie Louise. In some instances the ovules were killed.

Some leaf-buds showed blackening in the vascular bundles, but later, when cut shoots were left in water in a warm room, the buds were seen to push into growth.

The varieties particularly noted to have blackened pith in the 1-year-old shoots were Williams's Bon Chrétien, Beurré Hardy, Conference and Fertility. In scion wood of these varieties, cut for grafting in March, the pith and sometimes the cambium were black or brown, and had a water-soaked appearance. Further, whereas the bark usually adheres to the wood early in the year, it peeled off readily and tended to split when the grafts were made. Sometimes the blackening in the core of the wood was found at the top and bottom of the shoots, but not in the middle. The injury did not prove to be serious, since most of the scions eventually grew quite normally. In a propagation trial, out of a total of 2,321 Williams's Bon Chrétien scions worked direct on Quince A and C and with various intermediates, only 26 per cent. failed to grow, which is a low figure considering that a certain number of the combinations were known to be incompatible.

Other damage. Quince stool beds which had been unearthed before the severe weather set in were badly damaged, few surviving the winter; but those unearthed subsequently grew normally. Three *Bradley's King damson* trees developed frost cracks on the trunks with considerable areas of lifted bark on each side. The cracks were on the south side of the trees and extended vertically down the trunks. In some *loganberries* pieces of the outer rind of the canes became detached and slipped off when the canes were tied to the wires. This damage was not extensive although many canes were killed on 5-year-old loganberry plants.

Remedial measures and their results.

While it was not known how far the damage described above would prove deleterious to the trees under English conditions, experience in other countries had shown that, if not checked, the after effects of bark splitting and lifting might be serious. Experiments were therefore started forthwith to find out how the effects of the injuries could best be mitigated. These had three main objectives: (i) to prevent the drying out of the wounds, (ii) to prevent their extension, and (iii) to encourage callus formation, so that the wounds might heal quickly. The principal methods adopted were nailing down the cracked and lifted bark and sealing the wound.

Ninety-three Cox's Orange Pippin and nine Duchess' Favourite trees on Malling No. IX rootstock with 126 cracks in all, were treated by nailing the bark

down firmly to the wood by two rows of small-headed nails ($\frac{5}{8}$th inch, 20 gauge, gimp pins) on each side of the cracks, using a light hammer. Vaseline was applied to the cracks to prevent drying out. On some trees the nails were driven through small squares of rubber to prevent their heads from sinking into the bark. Thirty-four cracks were left unnailed for comparison. This method of nailing, long ago applied at Sinoleka, Poland, was described by Filewicz (1939) and Filewicz and Modlibowska (1940). Wallace (1929) recommended nailing.

The results of the measures taken were obtained from a comparative study of the behaviour of the treated and untreated trees made during the spring and summer of 1940, and they will now be described.

Measurements taken weekly on eight selected trees of Cox's Orange Pippin and Duchess' Favourite, four treated and four untreated, showed that most of the extension of the bark lifting occurred early in the year (February and March), whereas the maximum increase in width of the cracks occurred later (June). In general, the cracks increased in length and in width gradually, over a long period, especially in those unnailed, in which the cracks gaped widely, leaving an expanse of exposed wood. All the unnailed cracks increased extensively in length and width. Of the 104 cracks on the nailed trees of Cox's Orange Pippin 44 per cent., and of the 21 cracks on the nailed Duchess' Favourite trees 34 per cent., showed a comparatively small increase in length. The increase in length and width of the cracks in the unnailed trees continued for a longer period than in the nailed ones. Thus, in the former, it continued up to early and mid-July respectively ; in the latter, only to the middle and end of June. Similarly with bark lifting ; in the unnailed trees this continued up to mid-April, but in the nailed, up to the beginning of March only.

The average increase in length and width of the cracks in nailed Cox's Orange Pippin trees was 13 mm. and 7 mm. respectively, and, in unnailed trees 26 mm. and 20 mm. The average increase in width of lifted bark in the eight Cox's Orange Pippin trees, selected for detailed observation, was 51 mm. on those unnailed, and 18 mm. on the nailed ones. Amongst the Duchess' Favourite there was an average increase of 11 mm. and 17 mm. in width of nailed and unnailed cracks respectively. There was no difference in the increase of length of the cracks in nailed and unnailed trees of this variety.

In the unnailed trees, the bark was separated from the wood for a period of from 12 to 15 weeks, after which the area of lifted bark gradually became less as callus formation progressed ; the callus could clearly be seen after 19 weeks. Nailed trees, however, healed more quickly. Tapping with the hammer each week revealed that after 10 to 12 weeks the hollow area had diminished, and by the twentieth week, callus had formed a complete lining beneath the bark. In unnailed trees a certain width of lifted bark (as much as 39 mm. in one tree) always remained extending from the edges of the crack.

Sometimes the nails still held the bark down firmly a year after the cracks had occurred, but in some trees it had pushed through the inner row of nails, leaving them protruding from the wood. This was probably due to the thick growth of callus which usually extended practically to the edges of the flaps of lifted bark. This might perhaps have been avoided by the use of larger headed nails, placed further from the edges of the crack and by re-nailing later as the callus developed.

The bark had lifted from the nails in 41 per cent. of the Cox's Orange Pippin, and in 73 per cent. of the Duchess' Favourite trees. While callus had been formed in both nailed and unnailed trees, the former presented a neater appearance, and the callus afforded a more direct covering for the wood, protecting it from external influences such as adverse weather conditions, insects and diseases. (See Figs. 1 and 2, Plate I.)

From hand sections examined microscopically it was evident that the cambium attached to the loosened bark had produced both phloem and wood, whether the bark was nailed or not. In places where the bark was only slightly lifted the callus had united with the older wood in the spring of 1940. Where the air had exercised its drying effect on both the wood and callus surfaces and the latter had become covered with a cork layer, union of the old and new tissues did not take place.

The small squares of rubber used with some of the nails partially prevented the heads of the nails from becoming embedded in the bark. The tension near the inner row of nails by the edge of the cracks caused the nails to become slightly embedded, and here the rubber, being cut through, eventually fell off. On the outer row the rubber squares remained firmly fixed and there was practically no embedding. Up to October 1941 the general growth, foliage and fruit development of the damaged trees were apparently quite normal whether the cracks were nailed or not. It is hoped to continue the observations for a further period.

CALLUS FORMATION IN FROST INDUCED AND MECHANICALLY CAUSED WOUNDS.

An examination was made by one of us (I.M.) of the callus formed in wounds of apple trees caused (1) by the severe winter conditions of 1939-40, and (2) by mechanical means towards the end of April 1940.

Callus formation in frost-injured trees. Sections were made from frost-injured trees of Cox's Orange Pippin and Allington Pippin during February, March, April and May 1940, and July 1941. The sections cut in February showed that in both varieties the separation of the bark from the wood took place through the cambial zone close to the edge of the wood. Callus formation on the inner face of the bark began at the end of March 1940, when large, thin-walled, cells could be seen arising in fan-shaped formations from the phloem

rays, and a few smaller ones arose from cells between the rays. These formations correspond to the laterally broadened " wood rays " described by Steinmetz and Hilborn (1937). No callus was found on the wood.

At the beginning of April the formation of new tissue between the callus and the secondary phloem was observed. It was of cambial origin and gradually differentiated into normal phloem and xylem elements. It took place not only where the frost cavity was already filled, as in Steinmetz's and Hilborn's investigations, but also and mostly in wounds not yet healed. The new xylem elements were separated from the first formed callus by an irregular line of frost-injured cells (Bradford and Sitton, 1929). The callus remained as a parenchymatous layer which was clearly visible in sections made in July 1941, and corresponds to the " frost rings " described by Tingley (1936). As already stated, no callus was formed on the wood. This is in accordance with the observations of Sass (1933) on healing in apple graft unions, who stated that wood ray cells and other living xylem elements produce no callus.

Callus formation in mechanical wounds. On April 21st, 1940, the bark was lifted mechanically from pieces of uninjured 2-year-old wood of Cox's Orange Pippin and Allington Pippin, and they were kept in a moist chamber at room temperature until May 10th. Sections made then showed that, in contrast to wounds caused by frost, the break had taken place through undifferentiated cells at the edge of the bark, and that callus had formed on both the wood and bark. The callus on the wood was formed by the cambium or its derivative undifferentiated cells, whereas that on the bark was mostly in the form of fan-shaped groups of cells arising from the rays. These observations are in conformity with those of Sharples and Gunnery (1933), who found that the callus in mechanically injured plants of Hibiscus and Hevea developed on both bark and wood surfaces, and that it was formed predominantly from the medullary ray system. In apple trees, however, the medullary ray elements do not play a predominant part in the wood callus formation.

The difference between callus formation in wounds caused by frost and in those due to mechanical injury results from the difference in position of the line of cleavage ; in frost-induced wounds no meristematic tissue remains on the wood, but after mechanical injury enough of it is left on the wood to give rise to callus there. It should be noted that in the frost-injured trees the cambium was dormant, whereas in the mechanically injured ones the cambium was in an active state.

ACKNOWLEDGMENTS.

The writers wish to thank Dr. W. Filewicz for his guidance and collaboration throughout this investigation, and Mr. T. N. Hoblyn for his advice in presenting the results.

SUMMARY.

Observations on the nature and extent of injury to fruit trees at East Malling during the severe winter of 1939/40 are recorded and the results of the remedial measures tried are described.

Older trees suffered less than younger ones. No trees or branches were killed outright ; but cracking and lifting of the bark of the trunk, and sometimes of the crotch and branches, occurred in five varieties of apple, one of pear and one of damson. One-year-old wood, fruit- and wood-buds of pears were injured. The outer rind of loganberries suffered, and canes of older plants were killed. Unearthed quince stool beds were badly damaged.

Damage was greatest in the lowest-lying parts of the plantations, and most frequent on the sides of the trunks exposed to the S. and S.W. Apple trees which had a double dressing of potash suffered more than those with a single dressing. On the dwarfing rootstock Malling IX least damage occurred ; on the most vigorous ones it was considerable, but it was worst on the rootstocks of medium vigour.

Fastening down the loosened bark with small nails inserted in two rows on each side of the longitudinal cracks in the bark and sealing the cracks with vaseline proved a useful remedial measure, for healing was more rapid and satisfactory in nailed than in unnailed trees.

The uplifted bark carried the cambium with it ; callus formed on the inner surface of the bark and eventually new phloem and xylem were produced here. No callus formed on the wood. In bark raised mechanically from healthy trees in April, when sap-flow had already started, cleavage took place in the cambium itself, part of it remaining attached to the wood and the other part to the bark ; callus was produced from both portions.

In no instance was the winter injury so severe as to affect the subsequent development of foliage, growth or fruiting of the trees, which remained apparently normal up to October 1941.

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PLATE I.

Frost injury to Cox's Orange Pippin on Malling No. IX.
Photographed on August 2nd, 1940.

FIG. 1. Nailed trunk crack.

FIG. 2. Unnailed trunk crack.

PLATE I.

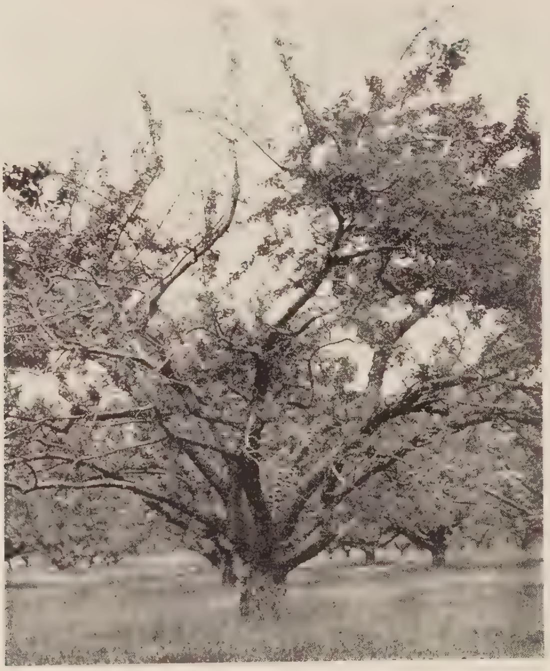

FIG. 1.
Bramley showing injury to lower branches (August 1, 1940).

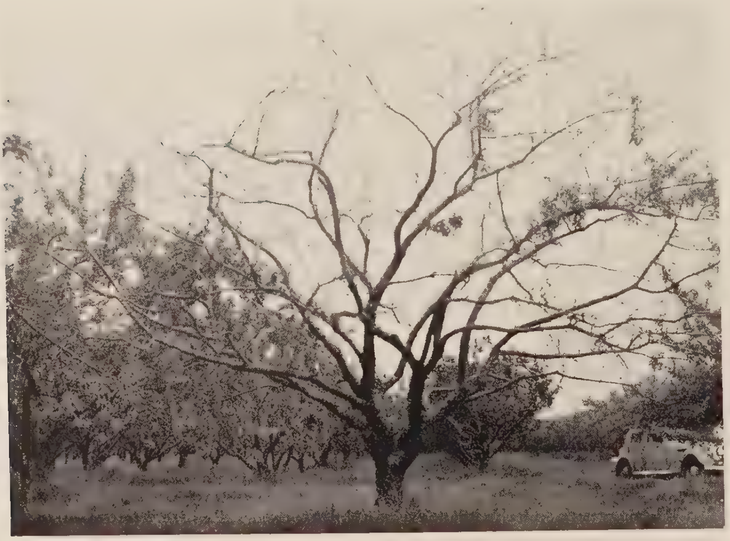

FIG. 2.
Bramley showing death of all but one or two small branches.
Note new shoots at crotch (August 1, 1940).

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NOTES ON THE WINTER INJURY TO FRUIT TREES IN ENGLAND, 1939-40

By C. E. CORNFORD* and N. B. BAGENAL
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In order to supplement the detailed observations at East Malling Research Station on the incidence of winter injury there, an attempt was made to gauge the extent and nature of the damage elsewhere.

First, a survey of some twenty-five Kentish fruit farms, selected for their special interest from a larger number on which injury had been reported, was undertaken. Second, questionnaires were sent to a number of selected fruit growers in the counties of Cambridge, Hants, Hereford, Kent, Norfolk, Surrey and Sussex, who had written to the Station reporting damage and seeking advice.

It cannot be claimed that either of these methods of enquiry was exhaustive or necessarily provided a typical sample representative of the state of affairs throughout the country. Indeed, the results of either enquiry by itself might have proved misleading. Considered together, however, they form a valuable addition to the preceding paper by Modlibowska and Field, in collaboration with whom and with Dr. W. Filewicz the questionnaires were drafted and analysed.

I. SURVEY OF WINTER INJURY ON SOME FRUIT FARMS IN KENT, 1940.

(C.E.C.)

In August 1940 the writer surveyed twenty-five farms from which interesting cases of winter injury had been reported.† The farms were examined with the special object of studying the influence of topography and altitude on the distribution of damage. It was found that on twenty-two farms the greatest damage was caused at the lower altitudes. Thus the topographical distribution of winter injury was similar to that of damage to fruit blossom observed after calm clear frosty nights during the spring.

The damage to Bramley's Seedling apple on a farm near Canterbury was typical. The orchards were planted on land which fell uniformly from an altitude of 170 down to 100 feet above sea level in a distance of three-quarters of a mile.

Four stages of damage were distinguished : (1) At the top of the slope the bark on the trunk was killed in irregular patches ; here there was a full crop.

* Working with a special grant from the Agricultural Research Council.

† He is indebted to Messrs. W. G. Kent and C. R. Thompson for bringing these farms to his notice.

(2) At an altitude of about 150 feet the bark on the trunk was killed in larger patches, and there were dead areas on the larger branches ; the crop was slightly reduced. (3) At an altitude of about 130 feet, the bark on the trunk was killed in irregular patches ; that on horizontal branches was killed all round ; the lower branches were dead ; the crop was very light. (4) At altitudes of less than 120 feet, the whole overground part of the tree was dead in August, except perhaps for one or two branches or twigs. See Plate I, Figs. 1 and 2. Most of these Bramley's Seedling trees were from 30 to 40 years old. The area of damaged orchard below an altitude of 130 feet was from 10 to 15 acres.

The fact that trees on low lying land were more damaged than similar trees on neighbouring higher land, about half a mile away, may be accounted for by the exceptional calmness and clearness of the night of January 19th-20th, 1940. It has been shown by experiments conducted by the writer* that on such nights the air in valleys cools to a lower temperature than air on neighbouring hills.

Of the twenty-five farms surveyed there were three, widely separated, on which fruit trees on high land were more damaged than those in neighbouring valleys. It is probable that this damage was caused on the more windy frosty nights which occurred in January. Experiments* have shown that on frosty nights, when the wind speed in the valley does not fall below three miles per hour, the hill air is colder than the valley air.

The exceptionally low air temperature recorded on the night of January 19th-20th was due to the simultaneous occurrence of calm air, clear sky and a layer of snow. At East Malling the snow was from three to six inches deep. The snow, being full of air spaces, is a poor conductor of heat and largely prevents the exchange of heat between the soil and the air. Thus, the air above the snow on the night in question had the best possible chance to cool. The 30 degrees of frost recorded in the screen at 4 feet above the snow was the lowest screen temperature recorded at East Malling during the twenty-six years that meteorological records have been kept there. At Wye, about nine miles from the orchard mentioned above, 34 degrees of frost were recorded in the screen. This was the lowest temperature recorded in the south-eastern counties during January 1940.

With regard to the relative susceptibility of the various kinds of fruit, Modlibowska and Field have described the damage found at East Malling Research Station on apple, pear, quince, damson and loganberry, but they found no damage on plum or cherry. On three farms near Canterbury severe winter injury was found on plum trees. The varieties affected were Monarch and President. The symptoms in order of increasing severity were as follows : (1) Tips of twigs dead ; no crop. (2) Whole trees apparently dormant from soil level upwards until June, when branches began to grow. (3) Whole trees

* *East Malling Research Station Annual Report for* 1938, p. 54.

quite dead from soil level upwards ; suckers springing up from still living roots and stock. Cherry trees suffering from winter injury were found in certain orchards near Faversham. The flowers of most of the varieties of cherry grown there were damaged in the bud, causing an almost complete failure of the crop.

On twelve of the twenty-five farms visited the older trees were definitely more damaged than young ones. In these instances the older trees were mostly Bramley's Seedling forty years or more old. On the other hand, Modlibowska and Field report that at East Malling Research Station older trees appeared to be less affected than younger ones ; but it must be remembered that there the damage was not so severe and that none of the trees was more than twenty-five years old.

This may partly account for the fact that on fifteen out of these twenty-five farms Bramley's Seedling was the most damaged variety, whereas at East Malling, where the trees were generally considerably younger, this variety was unaffected.

Next to Bramley's Seedling, Grenadier suffered most amongst the apple varieties on these farms.

In 1939 the fruit trees in Kent bore heavy crops. This may have been partly responsible for the severe nature of the injury. Blair* reported that in many cases, after a severe winter, trees which had cropped heavily died, while those which had not cropped survived.

II. SUMMARY OF ANSWERS TO QUESTIONNAIRES FROM FRUIT GROWERS, 1940-41.

(N.B.B.)

In April 1940 a questionnaire on the extent and nature of the damage and the means taken to deal with it was sent out to each of fourteen fruit growers in the various parts of the country already named, and in July 1941 a second questionnaire was sent to the same growers to find out what had happened since, as a result of splitting and lifting of the bark.

Answers to the questionnaires suggested that Cox's Orange Pippin was the worst victim, though other varieties reported to be affected were Laxton's Superb, Lane's Prince Albert, Newton Wonder, Grenadier, Lord Derby, Worcester Pearmain, Beauty of Bath, Charles Ross, Miller's Seedling, King of the Pippins, Early Victoria and Arthur Turner. It will be noted that the variety Bramley's Seedling does not appear in this list. The majority of these farms contained only comparatively young plantations and it seems probable that few of them had Bramley's Seedling of a comparable age to those damaged on the Kentish farms visited during the survey. Trees on Malling rootstocks Nos. I, II, IX,

* D. S. Blair, " Winter Injury to Apple Trees in Eastern Canada, 1933-35." *Scientific Agriculture*, **16**, 1935.

XVI and on seedling Crab were all mentioned. No strict comparisons of variety or rootstock can be made as information on the proportions of each planted and their location is not available.

The nature of the damage varied from small longitudinal cracks a few inches long to splits of three to four feet in extent. Seven of the growers had treated the damage by nailing, in the manner recommended by Filewicz and Modlibowska (1940) and had then covered the wound with petroleum jelly, grafting wax, indasco or some other sealing agent.

In nearly all cases the bark had been pushed away from the nails as a result of active callus growth. In one case, in which alternate nails in each line were not driven home flush, it was reported that " these held the bark down and that the callus overgrew the nails which are now completely out of sight ". The best results from nailing were obtained by using large-headed nails immediately after the damage occurred. In nine out of the fourteen cases growers reported further damage to their trees, subsequent to the bark splitting and lifting.

In two cases young trees of Cox on No. IX which were not nailed suffered severely. In the first, the split bark was bound with grafting tape and smeared with petroleum jelly. By the end of the summer of 1940 it was reported that " the bark had completely softened and died right round the stem to an average length of about 8 inches ". These trees were bridge-grafted in the spring of 1941 and in July of that year it was reported that " about half the trees were alive but looking yellow ".

In the other case some trees had the loose bark pared back and covered with vaseline and flowers of sulphur while others were left untreated. Here many split trees cankered and died, but of those which did not canker, those left alone callused better than those which had been pared.

Three growers reported that some of their trees which had been split by the frost became infected with Silver Leaf later.

In one case in Essex, mature trees of bush Cox's Orange Pippin which had been bark-split and left untreated had one or more branches which appeared to be dying or already dead in August 1941.

These two enquiries bring out clearly the wide range of varieties which may be affected and the serious permanent damage which may result from abnormally low winter temperatures.

(*Received* 23/9/41.)

STUDIES IN STRAWBERRY VIRUS DISEASES

IV. SYMPTOM EXPRESSION OF YELLOW-EDGE IN THE VARIETY ROYAL SOVEREIGN

By MARY E. KING and R. V. HARRIS
East Malling Research Station

1. Introduction.

In 1927 batches of vigorous and apparently healthy runners of three selected strains of Royal Sovereign strawberry were planted out at the East Malling Research Station for a cropping trial. In the following year considerable variation in size and vigour was rather unexpectedly found in the plants, both from strain to strain and from plant to plant within the strains. Single plant selection for health and vigour was then resorted to, and a propagation trial was started in 1928 with the object of obtaining a really uniform vigorous strain for experimental use, and eventually for commercial distribution. In this trial the behaviour of about 2,500 plants constituting clonal races of the selected individuals was observed and recorded (Rogers and Edgar, 1938). More uniformity was obtained than in the preliminary trial, but some of the plants still showed pronounced dwarfing accompanied by a yellowish discoloration of the leaves, particularly around their edges. It was proved that this condition could be transmitted experimentally by grafting (Harris, 1932, 1933) and it was therefore considered to be due to a virus disease. The prevalence of this disease, Yellow-edge, was found to be one of the chief factors limiting the commercial life of the Royal Sovereign strawberry, since many of the infected plants rapidly deteriorated ; and it was concluded that the most important basis of runner selection for propagation was freedom from virus disease (Rogers and Edgar, 1938). Later, it was shown by Massee (1935, 1936) that Yellow-edge was transmitted by the common strawberry aphis, *Capitophorus fragariae* Theo.

From this work it was concluded that in order to obtain strawberry runners of high standard of health, early recognition of the disease symptoms was necessary, and drastic elimination from the runner bed of all plants showing traces of the disease imperative. The Isolated Block method of planting out runners was therefore tried (Rogers, King and Massee, 1939) and with good results. Eventually an East Malling clone (Malling 35) of superior Royal Sovereign plants was extensively propagated for distribution to growers.*

* This clone, though a very vigorous one, was later found to be extensively and probably totally infected with another virus disease, Mild Crinkle ; more recently an entirely virus-free strain of Royal Sovereign has been discovered and is being propagated.

2. DEVELOPMENT OF SYMPTOMS IN RELATION TO PLANT ENVIRONMENT.

The early work on Yellow-edge in Royal Sovereign had shown that the symptoms were more conspicuous at some seasons of the year than at others. In England the disease is usually best seen during late summer and autumn, but also sometimes, for short periods, during May and June.

A similar if not identical disease, known as Xanthosis, was described in California by Plakidas (1927). He also found that the intensity of the symptoms varied during the season and was correlated to some extent with the prevailing temperatures. From field observations in different localities, and from pot experiments, he concluded that " Air temperatures of about 80° F., and higher, induce partial to complete masking of the symptoms ". He also agreed with Tomkins (1926), who worked on potato Mosaic, that prolonged exposure to high temperatures is not necessary for masking to occur, and he therefore used the maximum rather than the mean temperature for purposes of correlation. Except during periods of high temperatures, plants showed symptoms during the summer and autumn. In winter and spring, however, the plants showed no symptoms ; they appeared to recover temporarily and make good growth, but they collapsed suddenly during May. Plakidas ascribed the temporary recovery to " the beneficial effect of the dormant period of the winter months ".

In order to trace the development of disease symptoms throughout the season, a numerical scale for recording the relative intensity of the disease was adopted at East Malling, and from June or July until late autumn weekly records of the aspect of the plants were made. This scale was as follows :

0 ————	Healthy.			
1 ————	Suspicious symptoms of Yellow-edge.			
2 ————	Definite	symptoms	of slight	intensity.
3 ————	,,	,,	moderate	,,
4 ————	,,	,,	severe	,,
5 ————	,,	,,	very severe	,,

In Fig. 1, the symptoms shown by ten plants known to be infected with Yellow-edge are shown as recorded week by week during the summer and autumn of 1935 and 1936. The intensity of the symptoms shows two distinct types of variation. First, there are periods when they are especially noticeable ; certain plants can definitely be recognized as being infected with Yellow-edge, while others cannot with certainty. Secondly, there is variation in the type of symptoms shown by different individual plants at one and the same time. Some develop symptoms and continue to show them moderately to severely early in the year, while others remain apparently healthy or show only mild symptoms throughout the year. These differences are discussed more fully below.

In studying seasonal variation of symptom expression, the total symptom-intensity numbers of all the plants was plotted, and compared with the records of weather conditions. It soon became evident that temperature was not the sole factor controlling the appearance of symptoms, since periods in which they were difficult to discern did not always coincide with or immediately follow periods of high temperature. On the other hand, when symptoms had once developed early in the year, fresh rises in the symptom-intensity curve were

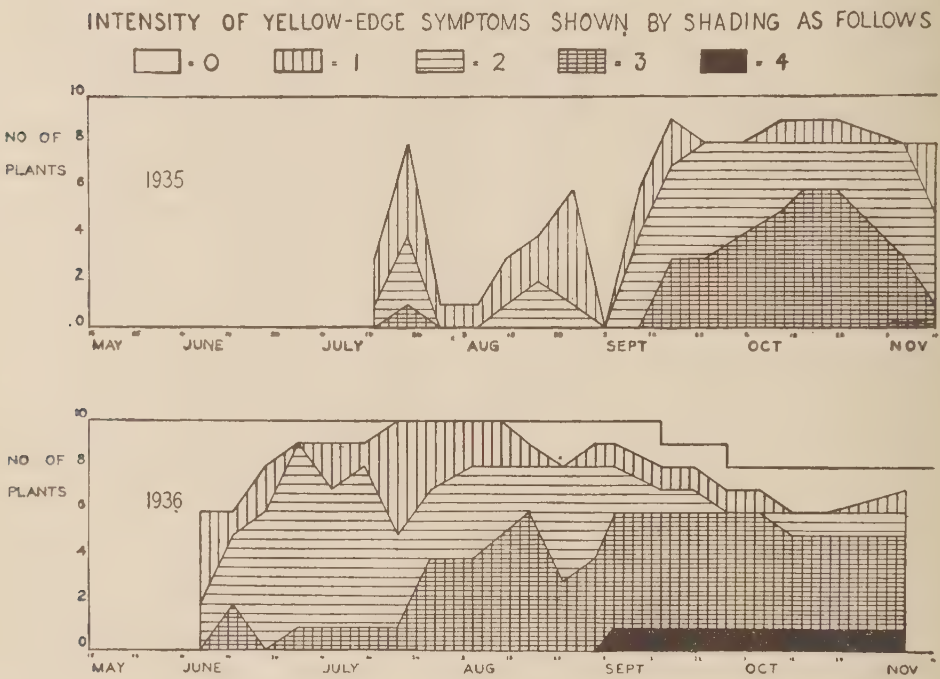

FIG. 1.

Symptom intensity 1935 and 1936, showing the number of plants in the different categories at weekly intervals.

nearly always associated with heavy rainfall which had followed periods of drought. This is well shown in Figs. 2 and 3. During this period it seemed that high temperatures were connected with symptom expression only when accompanied by drought, and that a reduction in temperature did not involve the reappearance of symptoms unless soil moisture increased at the same time.

A fuller explanation of the factors controlling symptom expression can therefore be obtained by considering the interaction of temperature and soil moisture throughout the year, and this may conveniently be divided into three phases. In the first, beginning in spring, soil moisture and temperature are

suitable for growth and development of new leaves, but the temperature is not high enough for symptom development. Diseased plants during this phase may differ from healthy ones only in their reduced vigour, but they are often indistinguishable from the latter if the disease has only recently been contracted. The second or intermediate phase begins when the maximum air temperature is about 60° F. or higher. This seems to be the minimum temperature for the appearance of symptoms in the early part of the season and is usually first reached during May. By then, however, soil moisture is often very low and has become a limiting factor preventing the appearance of symptoms. When soil moisture increases sufficiently, Yellow-edge becomes evident a week to a fortnight

FIG. 2.

Symptom intensity curves for infector and infected plants compared with weekly mean maximum temperatures and rainfall in 1936.
S1 = Infector plants (10 plants infected first in 1935).
S2 = Infected plants (10 plants grafted to infector plants in 1935 and showing symptoms for the first time in 1936).

later, but continues in evidence only so long as there is an abundant supply of moisture. This explains the occasional and temporary appearance of symptoms during May or June. This phase continues throughout the summer until the temperature falls below the critical point and once more becomes the limiting factor. The final phase, in which soil moisture is at saturation point then sets in, and the symptoms gradually fade away as the temperature gradually drops.

This was the conclusion suggested by the results obtained during 1935 and 1936 (Figs. 1 and 2), when the only information as to soil moisture

content was that provided by total rainfall figures. Since soil moisture depends also on other factors, such as rate of evaporation and rate of drainage, it was necessary to have a more reliable measure of it. In 1939, therefore, a Rogers (1935) soil tensiometer was installed in the row midway between two average sized plants. In Fig. 3 the symptom-intensity curve for 175 plants is shown against soil moisture and maximum earth temperature curves. The close correlation between the symptom-intensity and the soil moisture curves during the intermediate phase is particularly striking. The surmise as to the effect of

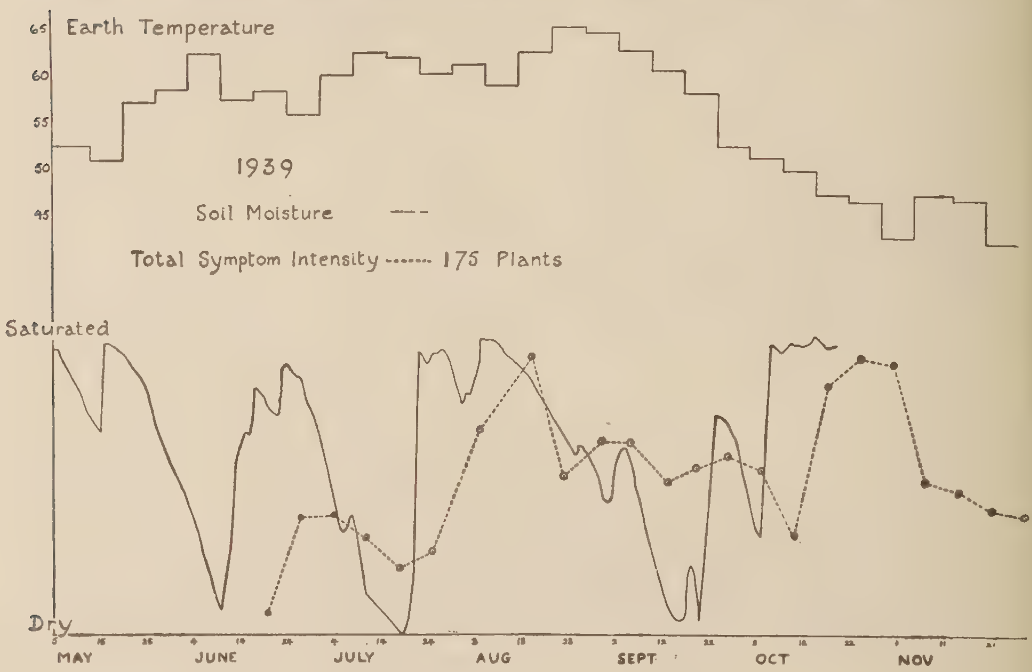

Fig. 3.

Symptom curve of A and B plants: earth temperatures, weekly means at 4 feet; soil moisture meter at 5 feet, daily 9 a.m. records.

weather on symptom development was thus confirmed. Further supporting evidence was provided by the behaviour of plants affected with Yellow-edge in the greenhouse. When the temperature was high enough for symptoms to develop they remained in evidence all through the summer (no matter how high a temperature was reached) until they finally faded out in late autumn. Such plants always had an adequate supply of moisture, hence symptom expression was never inhibited.

The young newly developed leaves show the symptoms most clearly, and the definite interval between the appearance of symptoms and the antecedent

occurrence of the weather conditions that favoured their development probably represents the time needed for these young leaves to be formed and to expand. To obtain further information on this point the rate of expansion of leaves was measured during the season of 1940. Four groups of Royal Sovereign plants which were, respectively, virus-free, infected with Mild Crinkle, with Severe Crinkle, and with Yellow-edge, were planted out at widely spaced intervals so that each plant was quite independent. Each week all newly expanded leaves were marked and counted, so that a record of leaf production from the very beginning of the season was obtained. It was found that the rate of expansion was very closely correlated in time with increasing soil moisture content. Apparently the effect of increased moisture is to stimulate young leaves already present in the crown to expand at once, but these leaves have passed the stage in which symptoms can be exhibited. Still younger leaves, formed whilst those just mentioned are expanding, are those that become visibly affected by the virus. This explains the time interval, and a clear distinction must be made between the formation and the expansion of leaves.

As the very young leaves that show symptoms of Yellow-edge grow older, the full complement of symptoms often becomes progressively more difficult to discern. The leaves take on a hard appearance and the yellow colour of the margin gradually disappears, so that curling of their laminae and stunting of their petioles are the sole symptoms that remain. This regression of symptoms is much accelerated if unfavourable weather conditions supervene.

The one great practical advantage of the interval to the grower is that it renders possible the forecasting of conditions suitable for roguing plants affected with Yellow-edge from runner beds. The weather during one week determines the aspect that the plants will present during the following week or fortnight. Much time and labour can therefore be saved by waiting for conditions under which the maximum number of plants show prominent symptoms.

3. VARIATION OF SYMPTOMS IN INDIVIDUAL PLANTS.

As a general rule infected plants gradually deteriorate and show symptoms of greater intensity the older they become. For example, in Fig. 1 the symptoms shown by the ten plants in 1936 were more severe and appeared earlier in the season than in 1935. Moreover, in Fig. 2 the upper curve represents the symptoms of the ten infectors, while the lower one represents that of the ten initially healthy plants grafted to them. Although the two curves are of similar type the symptom-intensities are distinctly different throughout, reflecting the two years' difference in age between the plants.

Although there is this general tendency for the symptoms to become more severe the older the plant or the longer it has been infected, all plants that show mild to moderate symptoms of Yellow-edge in their maiden year do not

necessarily become more drastically affected. Some, indeed, seem to be affected with a mild form of the disease which does not become progressively worse. Consequently the symptom-intensity amongst the individuals of a set of diseased plants may vary at one and the same time.

A suggested explanation of this was that differences in nutrition might account for these differences in individual behaviour. Supporting this idea was the fact that the wild strawberry (*Fragaria vesca* L.) had never been found naturally infected in the woods, although when potted up in the greenhouse or planted in an experimental plot it readily became infected both by grafting and by virus-carrying aphides. To test this idea a plot of ground in the woodland was cleared, cultivated and fenced, and twenty apparently healthy plants each of *F. vesca* and Royal Sovereign were planted out. Ten plants of each were allowed to produce runners unchecked, while runner production of the others was prevented. Before the plants could be infested artificially with captive viruliferous aphides so that their reaction to the disease could be tested, they had already been discovered by free flying aphides during the spring or summer migration periods, and the majority had already become infected with Yellow-edge. In a small piece of ground nearby, where the natural vegetation had otherwise not been disturbed, wild strawberries and Royal Sovereign planted in it had not been found by the aphides, and they remained healthy. The natural exemption of *F. vesca* from attack, therefore, seemed to be related to the habits and behaviour of the strawberry aphis rather than to a nutritional difference between cultivated loam and virgin woodland soil. In this connection the recent work of Greenslade (1941) on the migration of the strawberry aphis is of much interest.

A pot experiment was also carried out at the same time using (i) a good greenhouse compost, (ii) woodland soil, and (iii) peat from N. Ireland. Of both *F. vesca* and Royal Sovereign ten healthy plants and ten infected with Yellow-edge were grown in each type of soil, and the development and symptom expression were recorded. Differences in rate of development and amount of growth were noted between the plants in the three series of soils, especially with *F. vesca*, but no clear differences in symptom expression were seen. Symptoms were equally severe in the plants on all three soils and developed at about the same time. There was, in fact, far greater variation amongst the plants in any one soil type than in plants in different soils. Thus, the experiments showed that there was no simple nutritional explanation for the differences in intensity of disease that were found between plants.

The possibility that two or more strains of the virus differing in virulence might be involved was then examined. The strains of many plant viruses are mutually exclusive, and a plant infected with one strain is thereby protected from further infection by other closely related strains. These strains may differ

in virulence only, or in the type of symptoms they produce, and are found in widely separated categories of viruses, e.g. that of tobacco Mosaic, potato virus X and that of peach Yellows.

In a preliminary pot experiment designed to test this idea two clones of Royal Sovereign plants, one which appeared to be mildly, and the other severely affected with Yellow-edge, were used along with healthy plants of the Malling 35 clone. Mildly and severely affected plants were grafted together in pairs, using the stolon inarching method, while healthy plants were also grafted to each infector. Controls in which two mild infectors were grafted to each other, with a healthy plant grafted to each, were also set up.

In the controls the symptoms in all the infectors remained consistently of a mild type and only mild symptoms were transmitted to the healthy plants. Although the other clone comprised mostly severely affected plants a few showed only mild symptoms. Where a severely affected plant was used severe disease was transmitted to the mildly affected plant and to the two healthy plants, but where the ostensibly severely affected plant itself showed only mild symptoms, mild symptoms only were transmitted. This experiment, although not on a very large scale, does not produce evidence in favour of any protective action being exercised by the mildly affected plants against infection from the severely affected ones. On the other hand, it does show that there is a constancy in behaviour of the two different types of symptoms. Moreover, the experiment was carried out in the summer of 1938, and some of the plants were kept until autumn 1940 when each still showed the same type of symptom—intensity as at the onset.

Although the plants of the particular mild clone used in the above experiment behaved in a uniform manner and all of them consistently showed only mild symptoms, other clones, also derived from mildly affected parents contained in addition some plants showing severe symptoms. Similarly, some clones derived from severely infected parents gave mildly affected plants, as did the clone used in the pot experiment. Whatever type of symptoms was shown, however, was shown consistently, and no evidence of change over in a single individual plant was noticed. It seems possible, therefore, that if strains of virus are present at all they are present as a mixture, with the exception of the consistently mild clone, which may be pure. In any individual plant containing a mixture of strains one or other seems to become dominant and determines the type of symptoms shown. Further work on these plants must be done before any definite conclusions can be reached.

Bawden (1934) stated that protective action often breaks down when grafting is used for transmitting the various strains. On the other hand, Kunkel (1936) found no difficulty in showing a protective action by the virus of Little Peach against that of Peach Yellows, when using grafting methods of

transmission. Unfortunately no other method of artificial transmission of strawberry viruses is known at present, but parallel experiments were made using strawberry aphides to transmit the two types of symptoms. These, however, were inconclusive in two consecutive seasons, owing to failure to transmit any disease to many of the plants.

Fortunately there is some further evidence on the question of aphis transmission from a field experiment planted in the spring of 1938. Plants of clone Malling 35, free from Yellow-edge but affected with mild Crinkle, and plants mildly and severely affected with Yellow-edge were used in an attempt to find out whether any protective action was shown under field conditions. Eighteen five-plant plots of each of the three selections were planted out in randomized blocks in three rows, spaced as in a commercial fruiting plantation. Observations of symptom development and vigour were made in the 1938 and 1939 seasons. The healthy and the mildly affected plants grew well, but the severely affected ones lacked vigour from the start and were never comparable to the others in size or vigour ; many died or remained very dwarf.

No attempt was made to control aphides, as it was hoped that they would carry disease from one group to another, and information as to relative resistance to infection could thus be obtained.

In Table I, in which the results of the observations are summarized, only plants that were originally planted in the trial are considered. Certain gaps

TABLE I.

Relation of original virus status of plants to subsequent symptom expression, when exposed to natural infection conditions.

		Healthy.	Mild. 1 or 2.	Severe. 3, 4 and 5.	Misc.	
A. Malling 35	1938	32	38	14	6	90
(Mild Crinkle only) ..	1939	10	49	22	9	90
B. Mild Y-E.	1938	19	48	16	7	90
	1939	12	52	19	7	90
C. Severe Y-E.	1938	2	23	32	30	87
	1939	—	20	23	44	87

which occurred during 1938 were filled with similar plants, but these would not have been subject to the same chances of early infection. Intensity categories 3, 4, and 5 may be called severe infections, while 1 and 2 are mild infections.

From the results it is difficult to find any clear cut distinctions in behaviour. As is shown in Table I, the numbers of plants (A) originally healthy (except for mild Crinkle) and those of the mildly affected (B) plants placed in the mild and

severe groups in 1938 and 1939 are not markedly different, so that it does not seem that either set of plants is more liable to be resistant to further severe infection.

The set of severely affected plants (C) showed clear symptoms of Yellow-edge in both seasons, all except four showing a symptom-intensity number of 2 or more. Unfortunately many of them were so severely affected that they deteriorated into dwarf plants, to which a symptom number could not be assigned at all. This accounts for the great number classified as Miscellaneous in the Table. Some of these were also re-plants which are not comparable with the original plants as they would not have been subject to the same chance of infection by aphides.

The history of the A, B, and C sets of plants was analysed in detail, by following out the behaviour in 1939 of plants placed in the various categories in 1938. It was found that, on the whole, plants of the A and B sets classified as mild in 1938 were still mild in 1939, although some had become severely affected. In the same way, the smaller number of severely affected plants had also mostly continued as such. In fact, once again it appeared that a mixture of virus strains was present, and no apparent resistance was shown by mildly infected plants, as compared with healthy ones towards infection with more severe strains. It does appear, however, that when a plant is once infected and has shown typical symptoms, either mild or severe, in one season it tends to keep these symptoms in the following season ; although the symptoms may become one stage worse, they still remain within the same category.

Before the problem of strains of the Yellow-edge virus can be solved, selection of types must be intensified and more experiments made under controlled conditions. It may be possible to secure pure strains by sub-culturing several times, using single aphides feeding on small areas of leaf or for very short periods.

The question as to how these possible strains may have originated is also of great interest. Kunkel (1937, 1938) has shown that Peach Yellows may be controlled by heat treatment and that progressive inactivation of the virus of Aster Yellows in the body of the insect vector occurs with increase in temperature.

Most of the plants in the experiments here described had been warm water treated against the strawberry mite, and the possibility that mild strains had been induced by this means seemed possible. An experiment in which groups of plants infected with Yellow-edge were subjected to various heat treatments was therefore carried out, but no evidence of any change from mild to severe, or vice versa, was obtained. In the more drastic treatments there were some casualties amongst the plants, probably increased by a severe frost in the winter following treatment. Such plants as did survive, however, showed symptoms as severe as those shown originally.

4. Effect of Yellow-edge on the deterioration of Royal Sovereign.

(*a*) *Height and spread.* As with many other virus diseases, Yellow-edge of strawberries is associated with a stunting and dwarfing of the plants as a whole. The over ground parts of the plant are dwarfed to an extent determined by the intensity of disease symptoms shown by the plant. The size of all the leaf laminae is reduced and their petioles and inflorescence stalks become shortened. This leads to a flattened appearance of the plant as a whole.

A convenient method of following the changes in size of the plants is provided by the measurement of height and spread. The usual pomological

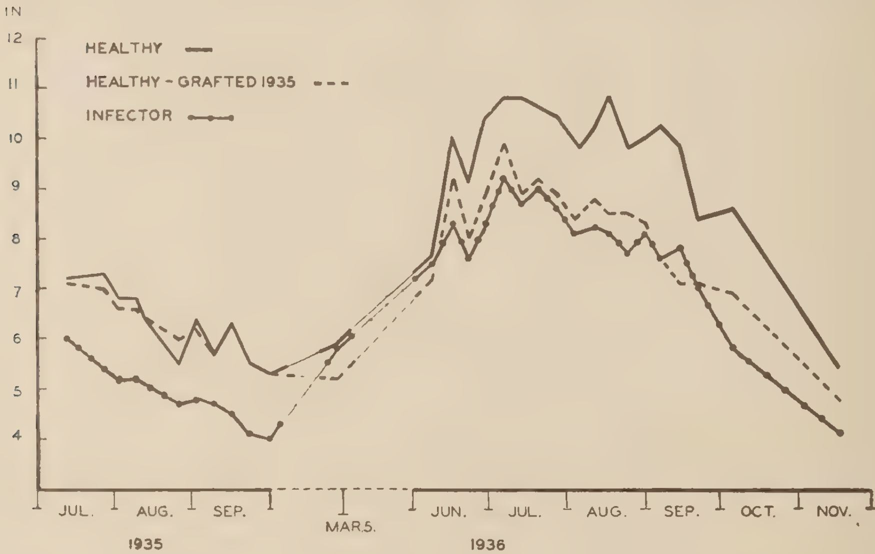

Fig. 4.

Average height in inches during 1935 and 1936 of healthy plants compared with infector plants and with healthy plants grafted to the infector plants in 1935.

methods are adopted, taking the height as that of the tallest leaf and the spread as the mean of two diameters of the area occupied by the plant, taken at right angles.

During 1935 and 1936 weekly measurements were made of the heights and spreads of the plants in an experiment in which twenty healthy plants and ten affected with Yellow-edge were planted out. Ten of the healthy plants were grafted to the ten diseased ones, the other ten remained ungrafted. In Fig. 4 the average heights of the plants in the three groups (i.e. healthy, healthy grafted to diseased, and the diseased to which the latter were grafted) are plotted throughout the seasons. The heights of the healthy and the diseased plants follow two distinct and approximately parallel curves, that of the diseased

being distinctly lower. The curve showing the height of the healthy plants grafted to the diseased (and thus contracting the disease) approximates closely to that of the healthy ones during the first season, but by the following year it has fallen to that of the diseased plants.

Curves showing the increase in the average spread of the plants show an exactly similar trend, except that that of the originally healthy plants infected by grafting does not approach so closely to that of the infected plants during the first season after infection. This confirms the observation that the immediate result of infection is a flattening of the plant followed later by reduction in size.

In other experiments measurements of height and spread have given similar results. In particular it has been shown that flattening and dwarfing increase as the intensity of symptom expression increases.

(*b*) *Runner production.* Plants affected with Yellow-edge show a considerably reduced vigour in the matter of stolon and runner production. When grown in pots, diseased plants produce very few stolons, while very severely diseased ones may not form any at all. If propagated out of doors, when root development is not restricted, more stolons and runners are produced, but not nearly so many as by healthy plants grown under the same conditions.

The results of an experiment in which the runner progeny was graded into three categories, according to size, are shown in Table II.

TABLE II.

Comparative runner production by healthy and diseased plants.

Group of plants.	Average No. per plant. Grade 1 and 2 runners, 1935.	Average No. per plant. Grade 1 and 2 runners, 1936.
Healthy, 1935 and 1936 ..	79 (10 plants)	{250 (5 plants)
Infected, 1936		{220 (5 plants)
Infected, 1935	53 (9 plants)	117 (7 plants)*

* In the second season (1936), five of the healthy controls were grafted to infectors. Two of the infected plants were grubbed on account of mite, hence the reduction in the number from 9 to 7.

There is a significant difference between all figures except the two bracketed together.

Here the numbers of plants in the two highest grades only, i.e. those which would be suitable for planting, have been used for comparison. The number of runners produced by the plants already infected with Yellow-edge in 1935 is significantly less than the number produced by the healthy plants in both seasons, 1935 and 1936, although the symptoms of disease were apparent only in a few cases in 1935. Although the number of runners produced by the plants infected in 1936 is less than that produced by the controls, the difference is not

significant. This is perhaps explained by the fact that the plants used as infectors had only a mild form of the disease.

5. Practical conclusions.

The selection and the propagation of clonal races of ostensibly healthy Royal Sovereign were started at an early stage in the present investigations. When the incidence of Yellow-edge disease was recognized as one of the chief factors in the rapid deterioration of the variety, routine inspection and the elimination of visibly affected plants and their progeny (roguing) from the runner beds became a regular practice, in order to maintain supplies of disease-free runners. The efficacy of the system depended on the relation between the time of infection and the appearance of clearly recognizable symptoms of the disease. In Royal Sovereign, high susceptibility is combined with well-marked symptom expression ; nevertheless, the symptoms at times are masked and this has been found to be related to the interaction of three factors, viz. :

(1) Seasonal weather conditions.
(2) Soil conditions, particularly soil moisture.
(3) The age of the infected plants.

Some of the plants that have become infected will generally show symptoms in early summer. This is usually followed by a period when the symptoms decrease, but they become more conspicuous again in the autumn. This fluctuation is related to temperature and soil moisture conditions. The expression of symptoms is encouraged by moist weather, and inhibited or reduced by hot dry weather. These observations suggest that preliminary roguing of established runner beds should be done in June and the final inspection and roguing in September and October. New plantings of runners should be inspected similarly and rogued.

Under uniform seasonal conditions maiden plants that become infected are less likely to exhibit symptoms of Yellow-edge than comparable two-year-old plants, so that roguing is likely to be more effective on two-year-old runner beds than on maiden ones.

SUMMARY.

1. The early observations on the incidence of the Yellow-edge disease of strawberries in the East Malling selections of the Royal Sovereign strawberry are reviewed.

2. The symptom expression of Yellow-edge is closely correlated with the interaction of temperature and soil moisture. Three phases may be recognized :

(1) In early spring soil moisture is adequate but temperature during this phase is not high enough for symptom expression.

(2) An intermediate phase begins when the minimum air temperature is about 60° F.; during this period soil moisture is often too low for symptoms to become evident, and this accounts for the occasional and merely temporary appearance of symptoms during May and June.

(3) The final phase supervenes as the temperature falls in late summer and autumn; and, although the soil may be saturated with moisture, the symptoms gradually fade away as the weather becomes colder.

3. Experiments have shown that there is no simple nutritional explanation for the differences in the intensity of Yellow-edge symptoms shown by affected plants.

4. In a field experiment the results suggested that a mixture of strains of the Yellow-edge virus might be present but that no resistance was shown by mildly affected plants towards infection with more virulent strains.

5. The first result of Yellow-edge infection is a flattening of the plants, followed later by reduction in size. The flattening and dwarfing increase as the intensity of symptoms increases.

6. Plants affected with Yellow-edge show considerably reduced runner production.

7. Symptoms begin to be evident a week to a fortnight after environmental conditions are such that the air temperature is above 60° F. and soil moisture supply is plentiful. Such periods, when the symptoms can most easily be detected, and when roguing is possible and should be carried out, usually occur in June and, especially, in early autumn (September and October).

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STUDIES IN STRAWBERRY VIRUS DISEASES

V. THE USE OF *FRAGARIA VESCA* L. AS AN INDICATOR OF YELLOW-EDGE AND CRINKLE

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INTRODUCTION.

In the study of plant virus diseases it is often important to know what particular virus or mixture of viruses is present in the plant under examination. Clearly marked symptoms characteristic of infection by a single virus may not always be evident because of the presence in the plant of another or of other viruses. Again, within one species of host plant there may be varieties which differ not only in susceptibility to initial virus infection, but also in the degree to which infection becomes manifest by recognizable symptoms of disease. In determining the viruses present in a plant it may be necessary to make transmissions from it to an indicator plant, that is, one that can easily be infected and will readily show the symptoms characteristic of a particular virus. In the strawberry this is particularly necessary when examining carrier varieties to determine whether selected plants of these varieties are virus-free or not. The terms susceptible and carrier as applied to host varieties are merely a matter of the relative degree of symptom expression or masking which they exhibit when infected, and no hard line can be drawn between them (Rogers, King and Massee, 1939). The only perfect (i.e. symptomless) carrier yet found amongst strawberries is *Fragaria chiloensis* Duchèsne. Huxley's Giant, a commercial variety reckoned as being nearly a perfect carrier, may show severe virus symptoms in its final stages of deterioration. Similarly Royal Sovereign, one of the most susceptible varieties, may carry the Yellow-edge virus, with symptoms entirely masked, at certain periods. In practice susceptible varieties are those which can be rogued effectively on field inspection, since the symptoms are fairly sure to be evident at some time or other in any one year ; carriers are varieties in which virus symptoms may be entirely absent or masked for a whole year or more, thus preventing fully effective roguing ; nevertheless in many carrier varieties field roguing is possible to a limited extent.

Several species of Fragaria and some of other genera have been tested for their suitability as indicators for strawberry viruses, and the wild woodland strawberry *Fragaria vesca* L. has proved, up to the present, to be the most useful in the experiments at East Malling. In a recent paper Hildebrand (1941), working with two American symptomless carrier varieties, records that certain

very susceptible strains of *Fragaria virginiana* Duchèsne proved to be suitable indicator plants.*

The present paper describes experiments in which plants of various strawberry varieties under trial at East Malling have been tested by grafting to possible indicator plants, and deals particularly with the results obtained on *F. vesca*. The experiments were carried out from 1935 onwards. The earlier ones have already been commented upon, although full details of them have not hitherto been published: the results obtained from them have been put into practice in the more recent ones.

METHODS OF GRAFTING.

So far as is known at present the only way of transmitting the viruses of Yellow-edge and Crinkle (apart from using the aphis vector, *Capitophorus fragariae*)† is by grafting. The method mostly used in these experiments was that of runner-inarching, a detailed account of which was given by Harris (1932). Various modifications have since been introduced and briefly referred to by Harris (1937*b*) and Harris and Hildebrand (1937), but they have not been published in detail heretofore.

The original method referred to as inarching—Method 2 (Harris, 1932)—consisted in inarching two stolons, one from each of a pair of parent plants, without removing either of the runner plants from the stolons.

Later, the grafting was simplified by the omission of the first cuts removing parts of the epidermis and cortex of each stolon, thus reducing the callusing surfaces to one-third; but this was found quite adequate for virus transmission. As described by Harris and Hildebrand (1937) "an improved binding medium was substituted for the old raffia and wax, namely, a proprietary sheet form of self sealing, pure crêpe rubber. With this material a graft union can be thoroughly sealed and bound rigidly and permanently in place in a single operation". In addition, small ties of this rubber bandage were used to bind the stolons together above and below the graft, thus removing any possibility of strain on the graft union itself. When callusing was complete the graft union was uncovered and left in position until transmission was seen to have taken place.

Originally the grafts were made with stolons whose runner plants possessed just visible root-initials. In later experiments the stolons used varied from those just completing their initial elongation to those whose runner plants

* This author found that under the conditions of his experiments the stolons produced by *F. vesca* were so thin as to make grafting impracticable.

† Since this was written Whitehead and Wood (1941) report having obtained transmission of Crinkle from Royal Sovereign to *Fragaria vesca* with *Pentatrichopus* (*Capitophorus*) *tetrarhodes* in 1940 and 1941; they suggest that there may be a "specificity of relationship between strawberry viruses and the genus Pentatrichopus".

showed their root initials. Stolons at a later stage of growth are too woody to allow of easy callusing, and grafts were attempted with these only when no other course was possible.

When this method was used out of doors, both in Canada (Harris and Hildebrand, 1937) and in England, it was found that the rubber bandage perished very rapidly and interfered with callusing. This was due primarily to the action of light rather than of high temperature, and various ways of protecting the rubber against light were tried. These included binding with raffia, covering with soil, painting with Indian ink and covering with tinfoil. The last method was found to be the most efficient and the simplest, and it has become the standard practice to cover all the main rubber bindings with tinfoil, whether out doors or in the greenhouse, since slow deterioration also takes place under glass.

The completed grafts were tied up to small canes using lead wire (Gauge 22), no attempt being made to establish the runner plants present on the grafted stolons in pots. All lateral branches of the stolons were removed as they were formed.

A further improvement was the use of special grafting knives instead of safety-razor blades. These, primarily intended for surgical use, consist of a metal handle with a thin detachable blade. When the blade becomes blunt another can quickly be substituted for it.*

These modifications provided a rapid and easy method of grafting strawberry plants, which involved only such a slight check to the stolons and their runners that failures were exceedingly rare. When failures occurred they were mostly due to mechanical causes, such as accidental severance of a vascular bundle, or great inequality in size of the two stolons. Occasionally rotting of the graft tongues occurred, due to excessive moisture, sometimes the result of grafting when the plants were wet either from watering or spraying. Failures were also sometimes due to the stolons being too old at the time of grafting.

The method described depends of course on the production of stolons by each plant required in the experiment. However, certain varieties and severely diseased individuals of others often produce no runners when grown in pots and cannot therefore be used for virus transmission by stolon inarching. Since such plants are often of great interest attempts were made in 1938, and developed further in 1939 and 1940, to graft leaf petioles instead of stolons.

Inarch grafts of young petioles of expanding leaves with young stolons from other plants were made. (See Plate I, Fig. 1.) The union was bound and covered in the usual manner. Callusing of the cut surface of the petioles was usually much less than that of the stolons, and since, in addition, the stolon

* Known by suppliers of surgical instruments as the Bard Parker Knife. Blade pattern No. 11 proved most suitable.

increased more rapidly both in diameter and length than the petioles a common callus was not always established. When this was formed, however, the union was sufficient to allow transmission of virus to occur, but the union was not of great mechanical strength.

A frequent cause of petiole graft failure was rotting of the graft tongues due to excessive humidity. Owing to shortness of the petiole the graft unions could not be raised much above soil level, and they were liable to become very damp. The arrangement of the graft union is shown in Plate I, Fig. 1, where successful union has resulted in the transmission of both Yellow-edge and Crinkle viruses from the Madame Lefebvre plant to the *F. vesca* indicator.

Petiole-stolon grafting is therefore a very useful supplementary method for the passage of virus from plant to plant. The chances of a successful union are not so great as in stolon-stolon grafting, but by using very young petioles and protecting them from rotting by watering the plants carefully, the proportion of successes can be increased. It is often possible by the use of such grafts to obtain valuable information which could not otherwise be secured.

General plan of the experiments.

After the Canadian work of 1933-34 (Harris and Hildebrand, 1937), in which it was established that some varieties commonly grown there were behaving as symptomless carriers of the Yellow-edge virus, experiments at East Malling were extended during 1935 to investigate the behaviour of certain species of Fragaria and Potentilla and of cultivated strawberry varieties other than Royal Sovereign towards the virus. The results of these experiments have already been briefly reported (Harris, 1937*a*; Harris and Hildebrand, 1937) and have been referred to in the report of parallel experiments in connection with Crinkle (Harris, 1937*b*). The work of later years has resulted directly from these initial experiments, accordingly the full results of the whole period 1935-40 will be presented here.

At first Royal Sovereign was the variety used as a standard source of infection and also as an indicator, but later work showed that the wild *Fragaria vesca* L. was more sensitive, and it has accordingly almost entirely replaced Royal Sovereign as an indicator.

Results.

1935-37 *Transmission Experiments.*

Plants of the varieties under test were combined with Royal Sovereign in two types of graft unit: (1) Test plants were stolon-inarched with healthy Royal Sovereign (Malling 35) indicators in order to determine the possible presence of virus in the former in spite of the absence of symptoms (symptomless carriers). (2) Royal Sovereign plants affected with Yellow-edge were stolon-inarched to

test plants, and these at one and the same time to healthy indicators, in order to obtain data on symptom expression in the variety under test. The main conclusions will briefly be indicated here, since later work depends upon them.

Fragaria chiloensis Duchèsne proved to be a symptomless carrier, none of the plants in any of the series showing symptoms of Yellow-edge at any time.* In Type 2 grafts Yellow-edge and Crinkle were passed through *F. chiloensis* to the indicator Royal Sovereign. Moreover the plants of *F. chiloensis* employed already contained viruses, since when they were grafted directly (Type 1) to Royal Sovereign indicators they induced Yellow-edge and Crinkle in them. By contrast, *F. virginiana* Duchèsne plants showed clear symptoms of Yellow-edge when grafted to infected Royal Sovereigns. Besides great differences in symptom expression there was also a great difference in the tolerance of the two species to the viruses. *F. chiloensis* remained strong and vigorous and showed no deterioration, while *F. virginiana* became severely affected, the plants becoming dwarfed and eventually dying out.

The wild strawberry, *Fragaria vesca* L., and various British species of Potentilla were also tested. Although a number of the Potentilla grafts were successful no transmission of virus was apparent, as no symptoms developed in any of the test plants or in the indicator Royal Sovereign. With *Fragaria vesca*, however, striking results were obtained. Not only in the Type 2 units was Yellow-edge shown by the test plants and transmitted through them to the Royal Sovereign indicators, but in the Type 1 unit another set of symptoms developed on *F. vesca*. In this graft unit, in which an ostensibly healthy Royal Sovereign was inarched to a plant of *F. vesca*, puckering and chlorotic speckling combined with some irregular curling of the laminae occurred on the latter. This indicated that Crinkle was present in the apparently healthy Royal Sovereign. Moreover, further examination showed that Crinkle symptoms were present along with those of Yellow-edge in the Type 2 graft units. Crinkle symptoms showed themselves only very slightly in Royal Sovereign, appearing as small and generally very inconspicuous groups of minute, chlorotic leaf lesions.

The final series of experiments, made in 1935, consisted in a preliminary test of the relative susceptibilities of some important commercial varieties and of some new seedlings raised by M. B. Crane. None of them showed the extremes of behaviour shown by *F. chiloensis* (symptomless carrier) and *F. virginiana* (pronounced symptoms). Nevertheless differences were apparent, some varieties tending to show symptoms more clearly than others. Moreover there were pronounced differences in tolerance.

* During one winter a few leaves on a small proportion of a clonal set of infected plants in an unheated glasshouse developed a slight and transient marginal chlorosis.

These preliminary experiments thus showed every indication of the existence of a series of susceptibility grades between the two extremes of the two parent species of cultivated strawberries, *F. chiloensis* and *F. virginiana*. Some varieties were symptomless carriers, others showed symptoms more readily, but no variety was found that had the complete tolerance of *F. chiloensis*. In addition, the discovery that *F. vesca* was a very sensitive indicator of Crinkle as well as of Yellow-edge opened up great possibilities for future work.

In 1936 and 1937 interest was concentrated on the reaction of *F. vesca* towards Yellow-edge and Crinkle, and on a survey of the incidence of mild Crinkle in the Malling 35 clone of Royal Sovereign and in other clones. It was found that mild Crinkle was universally present in all samples of Malling 35 tested, but the disease appeared to be of no commercial importance having little or no effect on the vigour of the plants or on their cropping capacity. Incidentally, no case of Yellow-edge was noted that was free from Crinkle. Crinkle, moreover, was not confined to Royal Sovereign but was found in other commercial varieties.

The use of Fragaria vesca as an indicator, 1938-1940.

(*a*) *Symptoms of Yellow-edge and Crinkle in F. vesca.* Having established that *F. vesca* was extremely sensitive to the viruses of Yellow-edge and Crinkle, the next step was to use it as an indicator for determining the virus content of other varieties and species. A single healthy plant of *F. vesca* was selected for propagation and from it a clone was established. A simplified graft unit was used, the plant under test being grafted to the *F. vesca* indicator and the symptoms read directly from the latter, no runners from it being propagated. This was found quite sufficient for reliable diagnosis, and the consequent saving in glass-house space allowed more tests to be made.

Crinkle symptoms shown by *F. vesca* vary in intensity according to the severity and the source of infection, but in all cases they include several different types of which one usually predominates. The two most prominent types are a dark green puckering of the leaf laminae, often accompanied by slight thickening in the darker green raised areas, and light yellow-green chlorotic spots which develop irregularly. In addition some twisting and curling of the laminae may develop, or they may remain flat and dwarfed and sometimes become strongly reddened in the region of the veins. The more severe the attack the more dwarfed the whole plant becomes, whatever type of symptom is dominant. The fluctuation in the type of symptom exhibited by Crinkle-infected *F. vesca* plants is difficult to understand ; plants of Royal Sovereign affected with mild Crinkle when grafted to healthy *F. vesca* may induce varied symptoms, sometimes puckering being more pronounced, at other times chlorotic speckling. The whole subject of Crinkle in Royal Sovereign and *F. vesca* needs further investigation.

From the point of view of plant-testing, however, the symptoms of Crinkle are well pronounced and easily distinguishable. In Plate I, Figs. 2 and 3, mild and severe Crinkle in *F. vesca* are shown.

The symptoms of Yellow-edge in *F. vesca* are less easy to classify, and it has sometimes been difficult to distinguish between plants infected with Crinkle alone and others infected with both viruses. Recent observations, however, have made diagnosis much simpler. Previously, the main diagnostic characters of Yellow-edge were the yellowing of the margins of the young leaves accompanied by curling and by the extreme dwarfness induced in the infected plants. Nevertheless, in *F. vesca* these yellowing and curling symptoms are never so pronounced as in Royal Sovereign infected with Yellow-edge.

During 1940 detailed observations were made, and all the *F. vesca* indicator plants were examined as frequently as possible. The symptoms of Yellow-edge and Crinkle developed by these plants were classified and grouped into three stages. Leaves showing Stage 1 symptoms develop from three to four weeks after grafting to a plant affected with Yellow-edge and Crinkle. These leaves are then not reduced in size, but the midrib of each leaflet is curled backwards and downwards, giving the whole leaf a rounded outline from a side view, as opposed to the normal flat appearance. They usually develop prominent, dark green raised up areas, due to continued growth of the mesophyll whilst that of the veins is restricted, and sometimes chlorotic speckling. The latter symptom is no doubt due to the Crinkle virus which is commonly associated with that of Yellow-edge. The curling of the leaves is the distinct feature due to the Yellow-edge virus and has not been observed on plants infected with Crinkle alone. On each *F. vesca* indicator plant one, two or three leaves may develop symptoms of this stage. These symptoms persist as long as the leaf remains and do not develop further.

Leaves in Stage 2 are not curled but are reduced to one-half or one-quarter the normal size. They are asymmetrical and the leaflets are sometimes arranged asymmetrically on the petiole. In addition, the usual symptoms of local laminal bulging (puckering), chlorotic spotting and reddening may be present. The number of such leaves is not limited and may often be greater than that of all other types of leaf, if the plant is not very severely affected. In Plate II, Fig. 1, an indicator plant (*F. vesca*), is shown in which most of the leaves are in Stage 2, while leaves in Stages 1 and 3 may also be seen.

Stage 3, the final stage, is not always reached. In this the leaves are extremely minute and the laminae are often very reduced in size or entirely absent. Sometimes these leaves do not even show typical Crinkle symptoms but are just very small, smooth, green leaves which are often reddened in the region of the veins. Plate II. Fig. 2, shows a *F. vesca* plant in which most of the leaves are in Stage 3, the laminae of all the previously healthy leaves and those

exhibiting Stage 1 having fallen off leaving the bare petioles. Frequently such a plant dies early.

It has been noticed that when a plant becomes infected by grafting to a diseased plant the viruses do not visibly affect leaves that have already developed fully, but only those that are still developing at the time of infection and those produced after infection has taken place. Presumably leaves that show Stage 1 symptoms are already partially developed at the time of infection, and the viruses have only a limited effect on them. This would explain the fact that only a few leaves become affected in this way. Later, the viruses may progressively interfere with the development of the leaves to such an extent that the plant can no longer survive.

With any of the stages described above, bending and twisting of the tips of young developing stolons may be present, as shown in Plate II, Fig. 1. If the stolon produces a lateral branch this is also twisted, even more than the main one. Young runner plants produced by these stolons are drastically affected, their leaves showing the symptoms characteristic of Stage 2 or Stage 3. Instead of elongating normally, such stolons grow very slowly and soon become thickened, hard and woody.

During experiments with diseased plants of the American strawberry varieties, Premier, Fairfax and Dorsett, some of them when grafted to *F. vesca* indicators induced in the latter symptoms of a distinctly different type which had not been seen before. In the indicator plants all the leaves were curled and dwarfed and were not puckered or chlorotic-spotted but were yellowish-green. The whole plant developed a matted, tussocky appearance. It is thought that this condition may be due to the Yellow-edge virus alone, without the complicating presence of the Crinkle virus. If this is so it will be of great value in finally elucidating the respective symptoms of Yellow-edge and Crinkle in *F. vesca*.

Thus by careful observation of the indicator plants (*F. vesca*) to which virus diseased strawberry plants are grafted, it is possible to diagnose the presence in them of Crinkle and/or Yellow-edge. Confirmation of some of the results has been obtained by grafting diseased plants to healthy Royal Sovereign plants as indicators, for this variety shows the symptoms of Yellow-edge much more distinctly than *F. vesca* does.

In view of the difficulties in diagnosing Yellow-edge in *F. vesca* various other species and varieties have been examined in the hope of finding a better indicator. These have included *Duchèsnea indica* Focke (a related species from N. America), Alpine strawberries and a new selection of *F. virginiana* from N. America. So far none of these has proved in the tests at East Malling to be as good as *F. vesca*, though recently Hildebrand (1941) reported that he had found very sensitive strains of *F. virginiana* that were good indicator plants.

(*b*) *Routine tests with F. vesca*. The experiments of 1935-37 indicated that strawberry varieties differed in their reaction towards Yellow-edge and Crinkle, some showing symptoms (susceptibles), others remaining unaffected (carriers). Consequently it was of great importance to determine by experiment and field observation the reaction of each individual variety towards these diseases. As a necessary preliminary to this work the collection and testing of samples in order to discover sources of virus-free plants of each variety was begun.*

During the examination of these samples with the help of *F. vesca* as indicator, some information as to the reaction of the variety was obtained at the same time. Since, however, all the plants sent in were chosen for their healthy and vigorous appearance, or because of their reputation for good cropping, there was less chance of receiving infected susceptibles than infected carriers. Consequently, among the susceptibles, most of the plants tested were either virus-free or infected with mild Crinkle only. On the other hand, most of the carrier varieties proved to be infected with both Crinkle and Yellow-edge.

Some of the main results of the tests are shown in Table I, and these will be discussed more fully under the headings : (i) Royal Sovereign, as representing a typical variety of the susceptible group, (ii) Huxley's Giant, a member of the carrier group, (iii) Other varieties, and (iv) New seedlings.

(i) *Royal Sovereign*. As has already been stated in the section dealing with the results of the 1935-37 transmission tests, the Malling 35 clone of Royal Sovereign and certain other good commercial Yellow-edge-free stocks were found to be infected throughout with mild Crinkle. As a result of a visit by Harris and Wellington to Ireland, samples from seven different sources of Royal Sovereign plants that had been grown in isolated localities since the time of the introduction of that variety were sent to East Malling for trial in 1938.† Of 94 of these plants grafted to *F. vesca* not a single one induced symptoms of Crinkle or Yellow-edge in this indicator, nor did they show any symptoms themselves.

Further plants from the Malling 35 clone and from a clone of Royal Sovereign affected with Yellow-edge were grafted in 1938 to *F. vesca*. Here the characteristic symptoms were shown both by the plants themselves and by the indicators. In both 1939 and 1940 similar results were obtained. All the affected Royal Sovereign plants showed symptoms, but the virus-free ones remained quite healthy. It was thus confirmed that Royal Sovereign is a variety susceptible to Yellow-edge and Crinkle and shows clear symptoms. Of the fourteen special

* The commercial importance of finding and multiplying virus-free clones of important varieties was also kept in view. A scheme was set in operation by which new clones of important varieties (where the virus test justified it) were subjected to pomological test and final multiplying up for commercial distribution. In addition to the stocks collected by the authors and their colleagues, samples from outstandingly good stocks in many areas have been sent in by County Horticultural Officers and growers, to whom the authors express their grateful acknowledgments.

† The authors record their great indebtedness to the late Professor Paul Murphy and his colleagues for invaluable suggestions and help in this connection.

TABLE I.

Plants of commercial varieties of strawberries tested in 1938-40 by inarching to Fragaria vesca.

Variety.	No. of sources from which samples were obtained.	No. of plants tested.	No. of successful grafts.	Symptoms in plants tested.			Symptoms in *Fragaria vesca* (successful grafts only).		
				No. of plants showing :—			No. of plants showing :—		
				Yellow-edge ± Crinkle.	Crinkle only.	No symptoms.	Yellow-edge and Crinkle.	Crinkle only.	No symptoms.
Royal Sovereign ..	14	167	164	25	36	106	23	35	106
Huxley's Giant ..	12	42	41	5	0	37	36	2	3
Sir Joseph Paxton ..	5	17	16	0	0	17	1	7	8
Improved Paxton ..	1	3	2	0	0	3	0	2	0
Tardive de Leopold ..	5	37	35	3	5	29	15	16	4
Madame Lefebvre ..	4	11	9	2	0	9	9	0	0
Oberschlesien	4	20	20	5	0	15	17	0	3*
King George	3	17	17	0	0	17	0	0	17
Western Queen ..	2	8	7	3	0	5	7	0	0
Deutsch Evern	1	5	5	5	0	0	5	0	0
Axbridge Early ..	1	1	1	0	0	1	0	1	0
Madame Kooi	1	3	3	0	0	3	3	0	0
Laxton	1	10	10	0	0	10	10	0	0
Scarlet Queen	1	1	1	0	0	1	0	1	0
Red Heart	1	7	7	0	0	7	7	0	0
Corvallis	1	5	5	5	0	0	5	0	0
Totals	57	354	343	53	41	260	138	64	141

* In further tests all of these transmitted Crinkle to *F. vesca.*

stocks tested, nine contained some virus-free plants. Plants from a clone raised from one of the best of these are now being distributed in quantity (Malling 40).

(ii) *Huxley's Giant.* This variety is widely grown and of great commercial importance. From field observations it has been noticed that although, as a rule, the plants seem tolerant of Yellow-edge and Crinkle, cases of rapid deterioration occur after one, two or three years with the development of symptoms reminiscent of Yellow-edge in Royal Sovereign. The cause of this is not yet fully known. During 1938 a selected sample of the apparently healthy Huxley, grown at the Research Station, was tested. It proved to be carrying the Yellow-edge virus. In 1940 numerous samples of this variety were obtained from different localities, requests being for vigorous stocks only. Altogether forty-two plants from twelve sources were finally tested. In no case did any symptoms develop on the Huxley's themselves, but all except four of the *F. vesca* indicators developed symptoms of Yellow-edge and Crinkle. Later (May 1941) two of these four indicator plants showed Yellow-edge and Crinkle, and the corresponding Huxley plants were discarded. The other two were retested in 1941 ; the indicator plant of one of them developed a slight trace of Crinkle but that of the other appeared to be free from symptoms. This apparently virus-free Huxley plant is now being propagated to form the most promising clone of this variety so far tested. Plate II, Fig. 3, shows photographs of four Huxley plants, two of which have already induced Yellow-edge and Crinkle symptoms on the indicator. None of the Huxley plants themselves shows symptoms of any kind ; this variety, therefore, may be considered as a typical symptomless carrier of both virus diseases. The results indicate the widespread infection of the variety.

(iii) *Other commercial varieties.* Virus-free clones of Paxton and King George have also been discovered and selected for propagation. Certain clones of other varieties have given promising results and are being given further trial. Yellow-edge-free but mild Crinkle-infected clones of Royal Sovereign, Paxton, Improved Paxton, Little Scarlet, Tardive de Leopold, and Axbridge Early have been found, but not all have been deemed of sufficient importance to propagate under present conditions. The plants of the clones affected with Crinkle do not necessarily show any external symptoms themselves and no data are at present available as to whether the presence of mild Crinkle causes any appreciable commercial deterioration. Paxton, in particular, rarely if ever shows any trace of Crinkle symptoms. One plant of Oberschlesien, which appears to contain the virus of mild Crinkle only, is the most promising yet found of this once very important variety.

A sample of plants from each of the affected clones tested during 1940 has been planted out in the field. Thus by observation of the behaviour of

individually tested plants some useful information as to the reaction of the variety towards Yellow-edge and the rate of degeneration, if any, may be obtained. During 1939 and 1940 experiments on these lines were begun with certain clones of Huxley, and subsequently some interesting cases of sudden deterioration have developed. Further experiments have been planned to study this problem.

The results of the tests of the varieties Huxley, Madame Lefebvre and Oberschlesien show that batches of plants from widely separated sources are almost invariably completely infected with Yellow-edge and Crinkle. The possibility of finding virus-free material of such varieties to employ as a nucleus for developing a healthy stock thus seems rather remote. Moreover the practical difficulties of roguing such a stock are very great, since most of the plants that happened to become infected would not show symptoms until a very advanced stage, and during all that time would themselves be sources of further infection. The only possibility of establishing a virus-free stock of a carrier variety is by propagating from tested material under vector-proof or vector-free conditions. Worn-out fruiting plants could be replaced from such a source. With susceptible varieties the position is much simpler ; since they do exhibit symptoms, it is possible to rogue out from propagation beds all diseased and suspicious plants soon after their infection, thus protecting the remaining plants from the disease. At the same time a nucleus of entirely virus-free material would, of course, be maintained under vector-proof conditions.

(iv) *New seedlings.* From time to time new seedlings and stray plants growing wild in neglected gardens and orchards have been sent for examination. In addition, promising seedlings developed by plant breeders have been sent in after preliminary horticultural selection. Tests of these with indicator plants showed that amongst such material, completely virus-free individual plants were not uncommon. Seedlings that had been grown on out of doors for some years by their breeder, however, had for the most part become infected with Yellow-edge and Crinkle, or with the latter alone.

It is unlikely that all the new seedlings tested were derived from entirely virus-free parents, owing to the scarcity of the latter. That the diseases in question are not transmitted through the seed is suggested by the discovery of virus-free individuals in recently introduced varieties, alongside of diseased ones. Seedlings grown for some time unprotected from aphis infestation showed a higher percentage of infection than protected ones : this indicates that a new seedling has little chance of remaining uninfected unless adequately protected.

Further evidence as to the non-transmission of the viruses by seed was obtained by a study of plants raised by the authors from seed. Seed of an established Alpine variety was sown but not one of the resulting seedlings developed symptoms of any kind, although it was proved by the grafting test

that they could readily be infected with Yellow-edge. In addition, seed sold as Royal Sovereign was sown and twenty-four individuals of the resulting mixed population were potted up. Before they were tested for the presence or absence of virus in the usual way some of them showed strongly suspicious yellowish leaf symptoms, but in no instance did any symptom of Yellow-edge or Crinkle develop in the indicators, so the symptoms were not of virus origin.

In a further experiment some thirty symptomless seedlings raised from the seed of a Royal Sovereign plant which had purposely been infected (by inarching) with severe Yellow-edge and severe Crinkle were tested in 1941. Not one of them induced the appearance of any virus symptoms in the *F. vesca* indicators.

Plakidas (1927) found that Xanthosis was not transmitted through the seed, while Chamberlain (1934) raised several hundred strawberry plants from seed of affected plants and not a single one showed any sign of disease.

Other possible indicators.

In view of the difficulty of diagnosing the symptoms of Yellow-edge in *Fragaria vesca* rapidly, the merits of other species of Fragaria and other strawberry varieties have been explored as possibly superior indicators for this disease. *Duchèsnea* (*Fragaria*) *indica* Focke, a wild North American species, was grafted to *F. chiloensis* carrying both Yellow-edge and Crinkle. Only two out of five grafts were successful, but the two *D. indica* plants showed pronounced symptoms of Crinkle, viz. prominent chlorotic spots. These symptoms, however, were exhibited only in the season of infection ; afterwards there was no apparent difference between diseased and healthy plants.

Seed of a Large Red Alpine strawberry was sown and a number of the resulting plants were compared directly with *F. vesca* by grafting a plant of each to an infected *F. chiloensis*. Pronounced symptoms of both virus diseases were shown by the Alpine plants, but they were no more easy to classify than those shown by the *F. vesca*. In addition, the stolons of the Alpine variety were far more liable to rot than those of *F. vesca*, thus making successful graftings very difficult.

Since in the early experiments in 1935 the Little Scarlet variety of *F. virginiana* was found to be extremely susceptible to Yellow-edge, a number of *F. virginiana* seedlings were raised from seed sent by G. M. Darrow from N. America. Each plant was duplicated by potting one of its runner plants, and this was then grafted to an infector. All the parent plants were kept isolated in an insect-proof greenhouse, so that if a suitable indicator were found amongst the runner plants its parent could be propagated to found a clone.

The seedling plants varied among themselves in leaf and floral characteristics and all were much more vigorous and possessed rougher and coarser leaves than the variety Little Scarlet itself which had been used in the earlier tests.

Their appearance agreed with the description of *F. virginiana* in Britton's North American Flora, and other workers refer to the variability in characters within this species, especially those of the flowers.

Two *F. virginiana* seedlings and one healthy *F. vesca* were compared by uniting each by a single graft to a Royal Sovereign plant affected with mild Yellow-edge. Twelve such sets of three plants each were completed. Symptoms of both Crinkle and Yellow-edge were rapidly shown by *F. vesca* but little or no effect was produced on the *F. virginiana* seedling, although the graft unions were quite successful. In a few of the seedlings slight Yellow-edge symptoms developed, but there was nothing to indicate the presence of Crinkle.

In passing, it may be mentioned that one of the fifty or so *F. virginiana* seedlings that were potted up showed pronounced symptoms of June Yellows, a disease considered to be genetical in origin. So far as the writers are aware this is the first time this disease has been observed in this species.

Conclusion.

The discovery in 1935 that *F. vesca* was extremely susceptible to the Yellow-edge and Crinkle viruses was confirmed in 1936 and 1937 and put to practical use in testing for the presence of these viruses in other strawberry species and varieties. By grafting a healthy plant of *F. vesca* to the one under test rapid diagnosis is possible, symptoms of virus present in the test plant being reproduced in the *F. vesca* plant.

During the progress of these tests it has been amply confirmed that strawberry species and varieties differ markedly in their resistance to, or tolerance of, these viruses. No hard and fast line can be drawn between tolerant and susceptible varieties ; they constitute, rather, a graded series from the very susceptible intolerants to those that tolerate and carry the virus without showing any symptoms at all. In varieties intermediate in behaviour between these extremes, it is impossible to be dogmatic as to what their reaction may be, since under some conditions symptoms may be produced and under others they remain masked.

Healthy looking plants of susceptible varieties such as Royal Sovereign, Paxton and Little Scarlet, have proved on actual test by grafting to be either completely free from the two viruses or else to contain only the virus of mild Crinkle. It has been possible to select from plants actually tested in the greenhouse and found to be virus-free, plants of important varieties such as Royal Sovereign and Paxton, and to build up new virus-free clones from them. Unfortunately it has not yet been possible to find virus-free plants of the long-established carrier varieties such as Huxley, Lefebvre and Oberschlesien, with the possible exception of the Huxley clone mentioned above (p. 237). Possibly the original presumably virus-free stocks of these varieties became infected soon

after their introduction ; this would explain why most of the stocks are now diseased. With further new varieties and seedlings, however, there is good ground for belief that virus-free plants could be selected and maintained, provided that they were procured and isolated at the time of, or very soon after, their introduction.

The chief problem that remains to be studied in connection with the widely distributed infected carrier types is the cause of the sudden breakdown in resistance to or toleration of the virus, resulting in their rapid deterioration. Were such virus-containing carriers not liable to this sudden deterioration, the fact that they contained virus would not be a disadvantage to those growers who preferred those varieties. On the other hand, such plants are a source of aphis-transmitted infection to any other strawberry plants grown in their vicinity.

Further experiments must also be made to examine the behaviour of the virus-free varieties towards Yellow-edge. This can be done by direct infection tests in the greenhouse and, where symptoms are shown, by field observations of plants infected by natural means.

SUMMARY.

1. A method is described of grafting strawberry plants by inarching stolons with stolons or with leaf petioles.

2. This method was used to determine the virus content of selected stocks of a number of varieties of strawberries by inarching plants of those stocks to healthy indicator plants.

3. Of several possible indicator plants tried the most satisfactory was the common wild strawberry, *Fragaria vesca* L.

4. Certain selections of the susceptible varieties Royal Sovereign, Sir Joseph Paxton and King George were found to induce no visible reaction in *F. vesca*, and were thus considered to be virus-free.

5. Selections of certain varieties that showed no symptoms of disease themselves transmitted disease when grafted to *Fragaria vesca* in which symptoms became evident.

6. Nearly all the selections of such carrier varieties induced symptoms in *F. vesca* and were, therefore, not virus-free, but one strain of Huxley's Giant appeared to be quite free from viruses and is being propagated for further trials.

7. Observations and experiments on possible seed transmission of strawberry viruses yielded negative results.

ACKNOWLEDGMENT.

The authors wish to thank Dr. H. Wormald for his invaluable help in arranging and editing this paper, and Dr. W. S. Rogers for numerous helpful suggestions. The unfailing interest and collaboration of both throughout these investigations is much appreciated. Thanks are specially due to Mrs. I. L. Painter for undertaking the manipulation of the experiments during a period in 1941 when both the authors were absent from the Research Station. They are also indebted to Mr. A. Tidy for his skilful care and manipulation of the plant material throughout the experiments. Thanks are also due to the Agricultural Research Council for a special research grant to aid the work.

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PLATE I.

FIG. 1.
A leaf-graft (petiole to stolon), showing transmission of both Yellow-edge and Crinkle from the Madame Lefebvre plant (left) to the *Fragaria vesca* indicator (right).

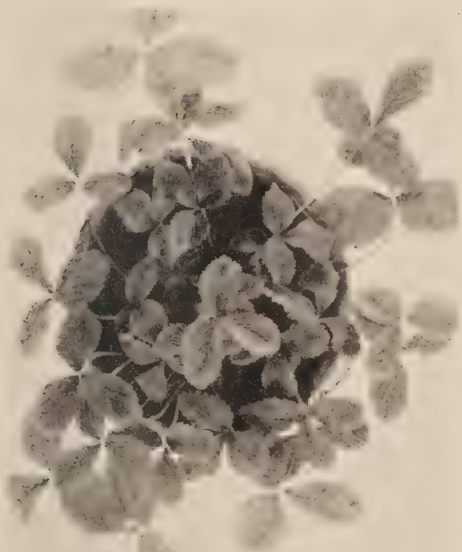

FIG. 2.
Mild Crinkle in *F. vesca*, transmitted from a plant of Malling 35 clone of Royal Sovereign.

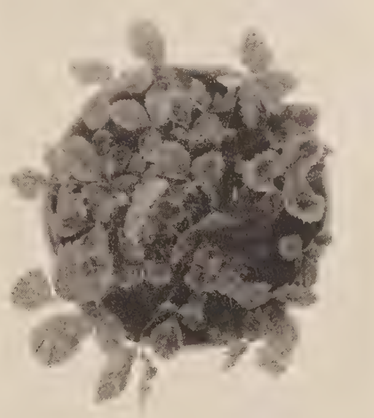

FIG. 3.
Severe Crinkle in *F. vesca*, transmitted from a plant of Malling 35 clone of Royal Sovereign.

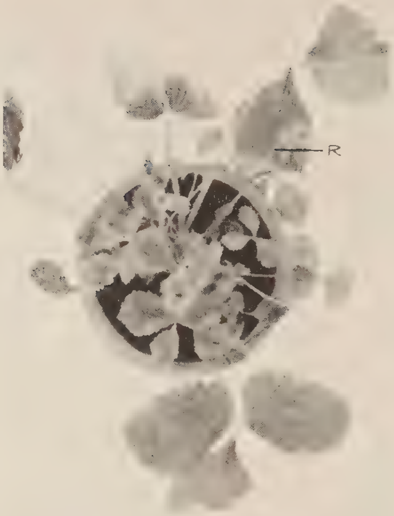

FIG. 1.

Fragaria vesca plant, as indicator, showing symptoms of Yellow-edge and Crinkle, transmitted from a plant of Tardive de Leopold with a trace of Crinkle. Note the curling of a young stolon at R.

FIG. 2.

F. vesca indicator showing Yellow-edge and Crinkle. Stage 3, transmitted from an apparently healthy Oberschlesien plant.

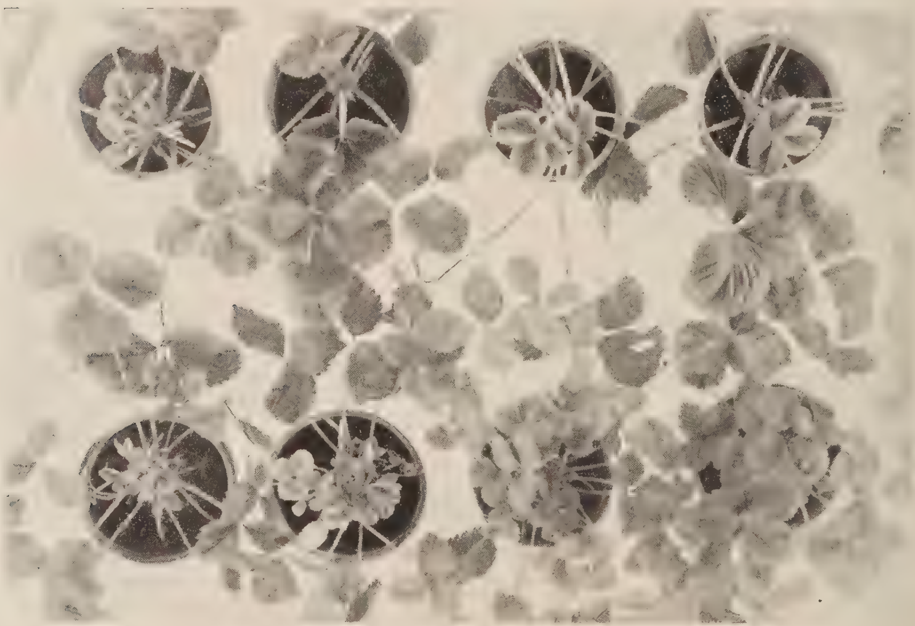

FIG. 3.

Four plants of Huxley's Giant apparently healthy (above) two of which have transmitted Yellow-edge and Crinkle to the *F. vesca* indicators (below); the other two Huxley's have not transmitted any symptoms.

REFRIGERATED GAS STORAGE OF FRUIT

V. CONFERENCE, DOYENNÉ DU COMICE AND WILLIAMS' BON CHRÉTIEN PEARS

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I. INTRODUCTION AND GENERAL SUMMARY OF RESULTS.

DURING the past six years (1934-40) a series of investigations have been carried out at the Ditton Laboratory on the reaction of home-grown pears to the composition of the storage atmosphere (1-8). As in the earlier work with apples, the investigations took the form of parallel storage trials in which different combinations of the three variables, (i) concentration of carbon dioxide, (ii) concentration of oxygen, and (iii) temperature, were used.*

While the range of concentration of oxygen and carbon dioxide over which satisfactory results can be obtained is fairly wide, the experiments carried out enable the optimum conditions of storage temperature and atmospheric composition to be defined with precision.

Each of the following varieties of pears was tested for at least two seasons, viz. Conference, Doyenné du Comice, and Williams' bon Chrétien.

In the following pages a detailed account of each experiment is given for purposes of record. The main results of practical importance can, however, be summarized as follows:

A very considerable extension of storage life can be obtained by the use of atmospheres containing lower percentages of oxygen (2·5 to 10 per cent.) and higher percentages of carbon dioxide (5 to 10 per cent.) than those normally present in air. Temperatures as low as 31·5° F. can safely be employed, pears appearing to be more tolerant of low temperatures than most varieties of apples. When storage temperatures as low as 31·5° F. are employed, the temperature of the fruit itself in different parts of the store should be very carefully watched to avoid risk of local damage due to freezing.

In contrast with apples, pears in cold storage or in refrigerated gas storage should not be wrapped in oiled papers. The wrappers do more harm than good.

Pears intended for storage are gathered in a hard, green and inedible condition. In the normal course of ripening in air at ordinary temperatures after

* The installation used for storage and the methods adopted in the handling, grading, and sampling of the fruit were similar to those described in Vol. XI (p. 149) of this Journal, except that the stored pears were not wrapped.

gathering, the above mentioned varieties undergo a change in ground-colour of the skin from green to yellow and a softening of the flesh. These changes begin soon after gathering and are accompanied by a rapid rise in respiratory activity (the climacteric rise). The melting-ripe condition of the flesh is reached at approximately the point at which the rise in respiratory activity reaches its maximum. In cold storage or in refrigerated gas storage very little change takes place in the ground-colour of the skin or in the consistency of the flesh. The rapid rise in respiratory activity to a peak value at which the fruit is in the melting-ripe condition, does not take place. Nevertheless, important changes do occur during storage, and these, if allowed to proceed too far, lead to failure of the fruit to ripen normally after removal from storage. If allowed to remain in storage still longer, the fruit dies and turns brown. There is no satisfactory means of judging from the appearance of the pears in store when they have reached the limit of their storage life, but a colour chart is included with this paper which shows the very slight change in ground-colour from green to yellowish-green which usually indicates the danger point.

The limits of storage life under the conditions of the experiments are given below for pears stored at various temperatures and in various gas mixtures; nevertheless, in view of seasonal variation, etc., the grower, if he desires to push the storage period to its limit, would be well advised to remove samples of fruit from store at intervals for a ripening test in air at higher temperatures.

The temperature for post-storage ripening or conditioning of pears is extremely important. A product of good quality cannot be obtained if the fruit is ripened at too high or too low a temperature; and when the fruit is nearing the point at which it will not ripen normally after removal from storage, the range of temperature at which satisfactory ripening can be obtained narrows towards the upper limit. The limits of temperature for satisfactory ripening are given in subsequent sections of this paper where detailed results obtained with each variety are set out.

The importance of the ripening temperature for pears should perhaps be stressed, because it is likely that fruit removed from storage during the winter months will be kept at temperatures too low for the development of optimum quality.

It was found that gas stored pears when ripened in air at 60° F. remained in the eating-ripe condition longer than similar pears ripened in air at the same temperature immediately after gathering. It was also found that the samples of gas stored pears showed rather more even ripening than the control samples.

Pears *must* be subjected to the correct gas storage conditions before the onset of the ripening phase that is indicated by the climacteric rise in respiratory activity, otherwise they will develop brown heart. The period available for handling the fruit prior to storage becomes shorter the longer the fruit is allowed

to remain on the tree. In normal circumstances *pears should be stored and the correct storage conditions established within four to five days of gathering.*

The experiments have shown clearly that the quality of pears when ripened after storage markedly improved the longer the fruit was allowed to remain on the tree. Pears picked prematurely usually fail to develop their optimum dessert quality. It would appear therefore that from the practical point of view the latest possible gathering combined with the utmost speed in bringing the fruit under the appropriate storage conditions are strongly to be recommended.

A point of practical importance is that the skin of pears that have begun to soften and to show definite signs of yellowing, is extremely delicate and susceptible to bruising. Even quite gentle handling may result in bruising and subsequent browning of the skin. This liability to skin damage is particularly marked in the Williams' variety. On the other hand, in the hard, green condition in which pears are removed from gas storage even this variety can be handled with little risk of bruising the skin.

II. CONFERENCE PEARS (1934-35).

GATHERING.

The pears were taken off 24-year-old bush trees grown on a good loam soil over brick earth at Faversham, Kent. Two pickings were made, the second approximating to the normal date for gathering this variety. At the first gathering (September 10th) the average size of the fruits was determined by eye, and all fruits were picked to this standard. At the same time similar fruits were labelled to serve as standards for the second gathering (September 24th). The average weights and average values for hardness, determined on 100 fruits, were as follows:

Date of gathering.	*Average weight.* (g.)	*Average hardness.* (lb. pressure on penetrometer.)*
10.9.34	126	14·2
24.9.34	146	11·0

Analyses of samples of the fruit immediately after gathering gave the following results, expressed as percentages of original fresh weight:

	Glucose.	*Fructose.*	*Sucrose.*	*Acidity as malic acid.*	*Alcohol-insoluble residue.*
1st gathering	1·751	5·384	1·086	0·168	4·620
2nd gathering	1·371	5·911	1·833	0·156	4·085

* The dimensions of the plunger are: diameter of head, which was slightly convex, 8 mm.; depth of penetration, 8·2 mm.

The respiratory activity of six fruits, from the time of gathering onwards, was determined individually at 53·6° F. (12° C.). The data are summarized in Table I.

TABLE I.

Respiratory activity at 12° C. (53·6° F.) of Conference pears (1934).

	Respiratory activity (cc. CO_2/10 kg./hr.).			Days from gathering to pre-climacteric minimum.	Duration of climacteric rise (days).
	Immediately after gathering.	Pre-climacteric minimum.	Climacteric maximum.		
1st gathering ..	65	45	145	12	23 (approx.).
2nd gathering ..	50	40	130	6	20 (approx.).

It will be seen that the fruit at both gatherings was in the pre-climacteric condition and was therefore from the point of view of maturity, suitable for gas storage.

Sampling, etc.

The methods already described were adopted for sampling. Each sample consisted of twenty fruits. The number of samples stored was thirty-six for each set of storage conditions. This allowed for six examinations, six samples being removed on each occasion.

A. Storage in air.

Conditions of storage.

The fruit was stored within twenty-four hours of gathering. The temperatures used were 34° F. (1·1° C.), 37·4° F. (3° C.), 41° F. (5° C.), 45·5° F. (7·5° C.), 53·6° F. (12° C.), and 64·4° F. (18° C.).

At the three lower temperatures the pears were stored on trays, in metal cabinets, ventilated with fresh air from outside the building. This air, before entering the cabinets, was conditioned to about 90 per cent. relative humidity. At the three higher temperatures the fruit was stored on trays stacked in constant temperature rooms, the air in which had a relative humidity of approximately 90 per cent. A small quantity of fruit exposed in a room with the relative humidity of the air at 90 per cent. saturation dries more quickly than the same quantity of fruit kept in a cabinet with a restricted flow of air entering at 90 per cent. saturation. Approximately the same rate of water loss was obtained in both cases by covering with damp towelling the fruit stored in the open.

All the fruit was unwrapped because earlier storage trials with pears had shown that no advantage was to be gained by the use of wrappers, oiled or plain.

THE RELATION BETWEEN TEMPERATURE AND MEAN DURATION OF LIFE IN AIR.

At all the temperatures tested, except the lowest (34° F.), the pears, after gathering, passed through the same changes, that is, from the hard, green condition, through firm-ripe, melting-ripe and over-ripe stages, to the condition at which the flesh becomes very soft, mushy and brown (popularly called sleepiness). This final change usually begins in the region of the core, but eventually spreads throughout the flesh. It has therefore been termed *core breakdown* (Plate III, Fig. 5).

These ripening changes are reflected in the changes in respiratory activity (rate of CO_2-production). This falls immediately after gathering but soon

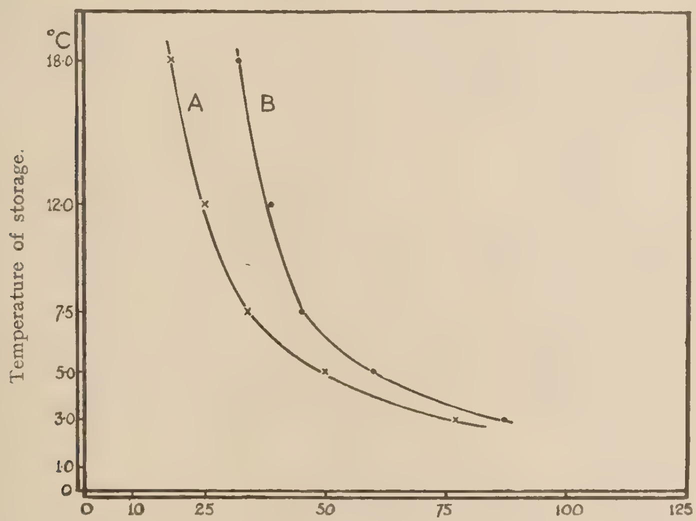

FIG. 1.
Days to ripen in storage.
Temperature and storage life of Conference pears.
A. First gathering (10.9.34).
B. Second gathering (24.9.34).

begins to rise (the climacteric rise) as the colour of the fruit changes from green to yellow and the flesh softens. The firm-ripe stage is usually reached before the respiratory activity attains its highest value. Maximum respiratory activity is associated with the stage at which the fruit is melting-ripe. The melting-ripe condition is short-lived and is succeeded by the over-ripe or sleepy stage which is accompanied by a definite fall in the rate of CO_2-production (Fig. 2).

The mean storage life is the point in time at which 50 per cent. of the pears are eating-ripe on the basis of several independent personal judgments. At this stage of ripeness the pressure recorded on the penetrometer was 2·6 to

2·7 lb. In no case did invasion of the fruit by fungi take place until it was well past the eating-ripe stage.

Data showing the relation between temperature and the mean storage life in air of the Conference pears of both gatherings are set out in Table II and Fig. 1.

TABLE II.

Mean storage life of Conference pears stored in air immediately after gathering, and ripened at the temperature of storage, 1934-35.

Date of gathering.	Temperature of storage.		Date when ripe.	Average life at storage temperatures (days).
	°F.	°C.		
1st gathering (10.9.34).	64·4	18·0	9 to 16.10.34	32
	53·6	12·0	18 to 20.10.34	39
	45·5	7·5	23 to 26.10.34	45
	41·0	5·0	9.11.34	60
	37·4	3·0	6.12.34	87
	34·0	1·0	did not ripen normally at this temperature	(113-140)*
2nd gathering (24.9.34)	64·4	18·0	9 to 15.10.34	18
	53·6	12·0	18 to 20.10.34	25
	45·5	7·5	26 to 29.10.34	34
	41·0	5·0	13.11.34	50
	37·4	3·0	10.12.34	77
	34·0	1·0	did not ripen normally at this temperature	(100-126)*

At 34° F. in air, as noted above, the pears did not ripen normally. They softened very slowly and eventually showed signs of yellowing. The softening that did occur was not sufficient to render them eating-ripe. At the same time they sweetened, but the sweetening was accompanied by an unpleasant aldehydic flavour. This condition was followed by browning and mealiness of the flesh after about six months' storage. If the pears were removed from the low temperature (34° F.) not later than approximately 3½ months from the date of gathering, they ripened normally at all three ripening temperatures tested, viz. 64·5°, 53·6°, and 45·5°. If kept at 34° F. for a further short period of about a fortnight they ripened normally at the two higher ripening temperatures but not at 45·5° F. After any further period of storage at the low temperature the pears, while still appearing firm and sound on removal, did not ripen normally, no matter what temperature was employed for ripening.

The breakdown and browning of the flesh characteristic of abnormal

* The figures in brackets denote the maximum periods the fruit can be kept at 34° F. and still ripen normally on removal to higher temperatures. In each case the two figures denote consecutive examinations, at the first of which the fruit removed to higher temperatures ripened normally, and at the second of which it failed to do so.

ripening induced by over-exposure to low temperature is here called *low temperature internal breakdown* since it appears in many respects to be analogous to low temperature internal breakdown in apples. This functional disease cannot be diagnosed in its early stages without cutting the fruit, and hard pears that are apparently sound, may be badly affected.

In spite of the bad effects of over-exposure to low temperature, pears can successfully be stored longer at 34° F. than at higher temperatures and may even be kept at 32° F. with a corresponding further extension of life.

The practical difficulty is to know when the fruit is approaching the stage of injury at these temperatures, in the absence of any marked visible signs. This difficulty occurs both in cold storage and in refrigerated gas storage. A slight paling or yellowing of the green ground-colour in cold storage or in refrigerated gas storage is an indication that the storage life of the fruit is nearly ended. On the accompanying chart Plate 3 indicates the probable limit of colour change it is safe to allow. Plate 4 indicates the stage at which some damage may have occurred.*

An interesting point emerging from the results of the storage experiments in air was that in all cases the earlier gathered fruit became eating-ripe about the same time as the later gathered fruit ; in other words, neither the fact of continued growth on the tree of the later gathered fruit nor the differences between the temperatures of storage used during the two weeks between the gatherings and the temperature of the orchard appeared to affect the result. It was found, however, that the later gathered fruit, when eating-ripe, was of a much superior quality to that of the earlier gathered fruit.

B. REFRIGERATED GAS STORAGE.

STORAGE CONDITIONS.

The pears used for the refrigerated gas storage trials were gathered at the same times and with the same precautions as those used in the experiments in

* The shades on this chart are based on Ridgway's Colour Standards, from which a selection of shades from green to yellow has been made at the Ditton Laboratory to cover the full range of ground-colour observed on apples and pears.

Ditton Laboratory Reference No.	*Ridgway's No.*
4	29′ (apple green)
4½	—
5	27′
5½	—
6	25′
6½	—
7	23′
7½	—
8	21′
8½	—
9	19′ (golden yellow)

The four shades reproduced on the chart included with this paper are Ditton Nos. 4½, 5, 5½ and 6.

air described above. They were stored at 34° F. (1·1° C.), 37·5° F. (3° C.), and 41° F. (5° C.) in the following atmospheres:

Atmosphere.	*Oxygen.* (%)	*Carbon dioxide.* (%)	*Nitrogen.* (%)
1	21·0	0·0	79·0 (Air)
2	5·0	5·0	90·0
3	2·5	5·0	92·5
4	10·0	10·0	80·0
5	2·5	10·0	87·5

The two gatherings were stored in separate cabinets. All the gas mixtures were made up by mixing the pure gases in the desired proportions and metering them through the storage cabinets at the required rate.* In all cases they were conditioned to approximately 90 per cent. relative humidity before entering the cabinets.

The fruit was not wrapped because it had already been conclusively shown that pears, in contrast with apples, can be gas stored satisfactorily without the use of oiled wrappers.

Six examinations were made of the fruit stored at 37·5° F. (3° C.) and 41° F. (5° C.) and seven of that stored at 34° F. (1·1° C.). At least three samples were removed from every set of conditions on each occasion.

Ripening or conditioning temperatures.

Under all the conditions of gas storage tested the pears remained hard and, with few exceptions, showed no appreciable change in the ground-colour of the skin over the whole period of observation. Little or no visible wastage occurred in the store. A comparison of the effects of the various storage atmospheres and temperatures is, therefore, not possible on the basis of the condition of the fruit on removal from storage. Any comparison must be based on a subsequent ripening test in air over a higher range of temperatures.

The temperatures used for ripening were 45·5° F. (7·5° C.), 53·5° F. (12° C.), and 64·5° F. (18° C.). Of these, the two higher ones produced equally good results, but the lowest one (45·5° F.) proved far less satisfactory. Not only was the quality of the fruit better when ripened at the higher temperatures, but the wastage was less. For example, there was on the average 4 per cent. and 5 per cent. wastage in fruit of the second gathering stored at 34° F. when ripened at 64·5° F. and 53·5° F. respectively, but 12 per cent. wastage when ripened at 45·5° F.

There is ample time for the marketing and disposal of fruit from refrigerated gas storage. Thus, the time taken to ripen after removal from storage at 34° F.

* This is known as the "continuous flow" method.

(average of all examinations of fruit of the second gathering, for all the atmospheres tested) was 12 days at 64·5° F., 16 days at 53·5° F., and 23 days at 45·5° F.

It is surprising that the time taken to ripen gas stored fruit, after removal from storage, does not become much shorter towards the end of the storage period but remains about the same throughout.

Gas storage results: comparison of atmospheres.

In making a comparison of the effect of the various atmospheres and storage temperatures tested, only the results obtained at a ripening temperature of 53·5° F. will be considered, since this is a very suitable one for the conditioning of Conference pears. The results obtained with the two gatherings of fruit are presented in Tables III and IV. These tables show the time taken to ripen after removal from storage and the quality of the fruit when eating-ripe.

Storage at 34° F.

It will be seen that with both the earlier and the later gatherings, the best results were obtained at the lowest storage temperature tested, viz. 34° F., and that all the atmospheres gave results which compared very favourably with those obtained in air.

Of the atmospheres tested, No. 3, consisting of 5 per cent. carbon dioxide, 2·5 per cent. oxygen and 92·5 per cent. nitrogen, was, on the whole, the best. Ripe fruit of excellent quality, with only 5 per cent. of wastage when ripe, was obtainable at the last examination, on July 4th. This fruit had, moreover, an effective period for distribution after removal from store.

In the other atmospheres at this temperature the fruit began to fail through abnormal ripening, i.e. a browning of the flesh starting at the core region and rapidly spreading throughout the cortex, after mid-April (1st gathering) and mid-May (2nd gathering). As compared with these results, the limit of the storage life of control pears cold stored in air at the same temperature was the end of January.

If storage beyond the end of April is not desired, atmosphere 4 (10 per cent. carbon dioxide, 10 per cent. oxygen, and 80 per cent. nitrogen) can safely be used. This atmosphere is similar to that used commercially for the gas storage of Bramley's Seedling apples, and is obtainable by the simple method of restricted and controlled ventilation. It is a less costly method than that required to produce atmosphere 3, since the latter can be obtained only by the use of some scrubbing device for removing the excess of carbon dioxide.

The dessert quality of the earlier gathered fruit was of a much lower grade than that of the fruit gathered at the normal time.

Table III.

Time (in days) taken to ripen at 53·5° F. (12° C.) by gas stored and cold stored Conference pears, and their quality when eating-ripe. (Fruit gathered 10.9.34.)

Storage temperature.	Days in store.	Composition of atmosphere.									
		Atmosphere 1.		Atmosphere 2.		Atmosphere 3.		Atmosphere 4.		Atmosphere 5.	
		CO_2 0·0% O_2 21·0% N_2 79·0%		CO_2 5·0% O_2 5·0% N_2 90·0%		CO_2 5·0% O_2 2·5% N_2 92·5%		CO_2 10·0% O_2 10·0% N_2 80·0%		CO_2 10·0% O_2 2·5% N_2 87·5%	
34° F. (1·1° C.)	113	10	f.	17	g.	16	g.	16	g.	20	f.
	140	8	p.	13	f.	16	f.	16	f.	18	f.
	179	did not ripen normally		15	f.	16	f.	16	f.	20	p.
	217			(14)	f.	(16)	f.	16	p.		
37·5° F. (3° C.)	72	6	f.	14	f.	16	f.	17	f.	20	f.
	84	5	p.	14	f.	16	f.	17	f.	19	f.
	112			13	f.	16	f.	17	f.	18	f.
	140			(13)	f.	15	f.	16	f.	17	f.
	179					14	f.	16	f.	18	f.
	217					14	p.	14	p.	18	p.
41° F. (5° C.)	63	3	p.	15	f.	16	f.	17	f.	20	f.
	84			(14)	p.	16	f.	17	f.	18	f.
	112					13	f.	13	f.	17	f.
	140					(11)	p.	(13)	p.	15	f.
	179									13	p.
	217										

g. = good. f. = fair. p. = poor.

Note 1.—Brackets indicate that wastage exceeded 10 per cent. when the fruit was eating-ripe.
Note 2.—Fruit assessed as poor should not be marketed, although there may be nothing in its appearance on removal from store to warn the grower of its poor quality.

TABLE IV.

Time (in days) taken to ripen at 53 5° F. (12° C.) by gas stored and cold stored Conference pears, and their quality when eating-ripe. (Fruit gathered 24.9.34.)

		Composition of atmosphere.									
		Atmosphere 1.		Atmosphere 2.		Atmosphere 3.		Atmosphere 4.		Atmosphere 5.	
Storage temperature.	Days in store.	CO_2 0·0% O_2 21·0% N_2 79·0%		CO_2 5·0% O_2 5·0% N_2 90·0%		CO_2 5·0% O_2 2·5% N_2 92·5%		CO_2 10·0% O_2 10·0% N_2 80·0%		CO_2 10·0% O_2 2·5% N_2 87·5%	
34° F. (1·1° C.)	99	12	g.	17	g.	17	v.g.	18	v.g.	19	g.
	126	9	f.	14	g.	15	g.	14	g.	16	g.
	165	5	p.	13	g.	17	g.	15	g.	20	g.
	203	did not ripen normally		10	g.	14	g.	13	g.	19	g.
	238			(11)	f.	16	g.	16	g.	(21)	f.
	283					17	g.	(18)	f.		
37·5° F. (3° C.)	58	6	g.	15	g.	16	g.	16	v.g.	18	g.
	70	4	g.	13	g.	15	g.	14	g.	15	g.
	98	over-ripe				15	g.	15	g.	(14)	g.
	126			8	g.	9	g.	(14)	g.	(14)	g.
	165			(9)	f.	(9)	g.	(14)	g.		
	203					(8)	g.				
41° F. (5° C.)	49	0	g.	13	g.	16	v.g.	16	v.g.	16	g.
	70	over-ripe		8	g.	11	g.	11	g.	(16)	f.
	98			(8)	p.	9	f.	(10)	f.		
	126					did not ripen normally		(7)	f.		
	165										

v.g. = very good. g. = good. f. = fair. p. = poor.

Note 1.—Brackets indicate that wastage exceeded 10 per cent. when the fruit was eating-ripe.
Note 2.—Fruit assessed as poor should not be marketed, although there may be nothing in its appearance on removal from store to warn the grower of its poor quality.

Table V gives the results obtained by measurements of the firmness of the flesh of the fruit stored at 34° F. It will be seen that the fruit stored in air at this temperature softened rapidly as compared with that in gas storage. In fact, after nearly eight months' storage most of the gas stored pears were slightly harder than at the time of gathering.

STORAGE AT 37·5° F.

This temperature can be used for storage until the end of March. At this temperature the best results were obtained in atmosphere 4 (10 per cent. carbon dioxide, 10 per cent. oxygen, and 80 per cent. nitrogen). Atmosphere 3 (5 per cent. carbon dioxide, 2·5 per cent. oxygen, and 92·5 per cent. nitrogen) was almost as good as 4, but it should be borne in mind that the latter is obtainable by control of ventilation alone and does not need any scrubbing device.

TABLE V.

Changes in firmness of flesh of Conference pears (lb. pressure on penetrometer) during storage in various atmospheres at 34° *F.* (*Gathered* 25.9.34.)

Days in storage.	Composition of atmosphere.				
	Atmosphere 1.	Atmosphere 2.	Atmosphere 3.	Atmosphere 4.	Atmosphere 5.
	CO_2 0·0 O_2 21·0 N_2 79·0 Air	CO_2 5·0 O_2 5·0 N_2 90·0	CO_2 5·0 O_2 2·5 N_2 92·5	CO_2 10·0 O_2 10·0 N_2 80·0	CO_2 10·0 O_2 2·5 N_2 87·5
0	11·0	11·0	11·0	11·0	11·0
98	10·4	—	—	—	—
119	8·5	—	—	—	—
164	5·8	11·6	11·8	11·3	11·1
202	5·0	10·5	10·2	11·3	10·9
237	4·6	9·7	11·1	11·2	12·5
282	—	9·3	9·8	11·5	11·7

STORAGE AT 41° F.

Gas storage at 41° F. has little to recommend it. Atmosphere 4 gave the best results, the fruit keeping fairly well until January. However, no better results can be obtained by gas storage at this temperature than by storage in air at 34° F.

BROWN HEART.

In the course of these gas storage trials with Conference pears only a small amount of brown heart was observed. It developed early in the storage life of the fruit and tended to increase with time in store. Table VI shows the percentage of fruits affected under each set of storage conditions. It will be

noticed that in the pears of the first gathering brown heart developed only to a very negligible extent. The injury was mainly confined to small areas in the region of the core. With fruit of the later gathering there was more brown heart, but at 34° F. it was still negligible from the practical point of view. It appears that higher storage temperatures, higher percentages of carbon dioxide and lower concentrations of oxygen are all associated with increase in brown heart.

TABLE VI.

Brown heart in gas stored Conference pears (1934).

Date of gathering.	Storage atmosphere.	Brown heart (%). Temperature of storage (°F.). 34°	37·5°	41°
12.9.34	(2) 2·5% oxygen, 5% carbon dioxide	0·1	0·0	0·4
	(3) 5% oxygen, 5% carbon dioxide	0·4	0·1	0·0
	(4) 2·5% oxygen, 10% carbon dioxide	0·0	0·4	0·6
	(5) 10% oxygen, 10% carbon dioxide	0·5	1·7	2·3
25.9.34	(2) 2·5% oxygen, 5% carbon dioxide	3·0	2·0	3·7
	(3) 5% oxygen, 5% carbon dioxide	0·8	1·0	0·1
	(4) 2·5% oxygen, 10% carbon dioxide	5·0	12·3	15·8
	(5) 10% oxygen, 10% carbon dioxide	3·0	4·3	4·1

III. CONFERENCE PEARS (1935-36).

In this season two gatherings of Conference pears were made, on 17.9.35 and 25.9.35 respectively, off 20-year-old trees, grown on a light loam soil containing a certain amount of sand and gravel.

The results of the storage trials confirmed those obtained in the previous season and did not contribute any new facts of importance. The data have therefore been omitted from this paper.

IV. CONFERENCE PEARS, 1938-39.

THE IMPORTANCE OF MINIMIZING DELAY BETWEEN GATHERING AND STORING.

Apart from the actual storage conditions, the most important factors in the cold storage or gas storage of pears are the stage of maturity at which they are gathered and the amount of ripening that occurs in the interval between gathering and storing. In all the experiments reported above the fruit was stored within twenty-four hours of the time of gathering and, in addition, the storage conditions, as regards both temperature and atmospheric composition, were established within about twenty-four hours of placing the fruit in storage. Under practical conditions, however, it is often not possible to gather and store pears in quantity as quickly as this. An experiment was therefore conducted in which the storage life of Conference pears, gathered on September 19th, 1938,

and stored immediately, was compared with that of fruit gathered on the same day and kept for 4, 10 and 13½ days respectively at 53·5° F. (the average temperature of the orchard) before being placed in store. The storage conditions used were cold storage (air at 34° F.) and gas storage (5 per cent. carbon dioxide, 2·5 per cent. oxygen, and 92·5 per cent. nitrogen at 34° F.). The date of gathering was about the normal one for the season.

A record of the respiratory activity in air at 53·5° F. of the fruit after gathering is given in Fig. 2. It is seen that the pre-climacteric minimum rate of respiration was reached 5 to 6 days after gathering. Reference to this figure will show the extent to which the respiratory activity had changed after delay in air at 53·5° F. for 4, 10 and 13½ days respectively.

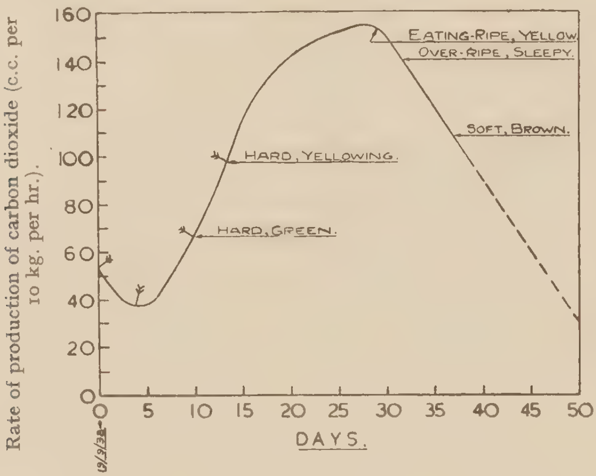

FIG. 2.

Respiratory activity in air at 12° C. of Conference pears from time of gathering (19.9.38).

Note.—The short arrows indicate the dates on which samples of fruit were transferred to cold storage and to refrigerated gas storage.

The storage results are presented in Table VII. The fruit delayed for four days in air at 53·5° F. gave nearly as good results as that stored immediately (Plate I, Figs. 1 and 2). Pears delayed ten days, although still hard and green when placed in storage, were in marked contrast and stored badly (Plate II, Fig. 3). Those delayed 13½ days showed a slight change in ground-colour and were kept in gas storage only. They were a complete failure in storage (Plate II, Fig. 4). The cause of the failure in storage after more than four days' delay in air at 53·5° F. was low temperature internal breakdown in the cold stored fruit, but brown heart in the fruit that was gas stored.

TABLE VII.

Effect of delay between gathering and storing Conference pears. (*Gathered* 29.9.38.)

Interval between gathering and storage (days in air at 53·6° F.).	Date of removal from storage.	Days in store.	Condition of fruit on removal from storage.		Time to ripen in air at 60° F. (days).	Condition of fruit when eating-ripe.		
			Hardness* (lb.).	Ground-colour† (Ditton Reference No.)		Percentage of flesh showing internal breakdown or brown heart.	Quality of the sound flesh.	Remarks.
Cold storage (Air at 34° F.).								
0	16.11.38	58	—	5	11	Nil	Good	Marketable
	5.12.38	77	12·8	6	10	Nil	Good	Marketable
	26. 1.39	129	8·5	6	9	Nil	Good	Marketable
	29. 3.39	191	7·7	7½	6	20 (slight)	Poor to fair	Unmarketable
4	16.11.38	54	—	5	11	Nil	Fair to good	Marketable
	5.12.38	73	13·2	5½	9	Nil	Fair to good	Marketable
	26. 1.39	125	8·5	7	8	8	Fair to good	Marketable
	29. 3.39	187	7·0	8	6	20 (slight)	Poor to fair	Unmarketable
10	4.11.38	36	—	6	7	4	Poor to fair	Unmarketable
	5.12.38	67	4·3	6½	4	52 (slight to severe)	Poor	Unmarketable
	26. 1.39	119	3·7	7	—	100 (severe)	—	Unmarketable
	29. 3.39	181	2·8	7	—	100 (severe)	—	Unmarketable
Gas Storage (5% CO_2 + 2·5% O_2 + 92·5% N_2 at 34° F.).								
0	15.11.38	57	—	5	17	3·5	Good	Marketable
	5.12.38	77	13·9	5	16	3·8	Good	Marketable
	26. 1.39	129	13·2	5	14½	6·5	Good	Marketable
	29. 3.39	191	13·1	5½	14	8·4	Fair to good	Marketable
4	16.11.38	58	—	5	16	8·0	Good	Marketable
	5.12.38	77	13·4	5	15	5·8	Good	Marketable
	26. 1.39	129	13·2	5	13	7·1	Good	Marketable
	29. 3.39	191	13·4	5½	13	8·4	Fair to good	Marketable
10	16.11.38	58	—	5½	11	53·0	Fair to good	Unmarketable
	5.12.38	77	—	5½	11	44·0	Fair	Unmarketable
	26. 1.39	129	7·5	5½	10	46·0	Fair	Unmarketable
	29. 3.39	191	8·9	6½	10	60·0	Poor	Unmarketable
13½	14.11.38	56	—	6	9½	72·0	Poor	Unmarketable
	5.12.38	77	—	6	?	100·0	—	Unmarketable
	26. 1.39	129	—	6	?	100·0	—	Unmarketable
	29. 3.39	191	—	—	?	100·0	—	Unmarketable

* Hardness when gathered = 13·8 lb. † Ground-colour when gathered = 5.

This experiment shows that if serious trouble is to be avoided, pears must be placed in store and the appropriate storage conditions of temperature and atmosphere established before the beginning of the climacteric rise in respiratory activity. The longer the fruit is left on the tree the shorter is the time available for getting it into the store before this critical change begins. Unfortunately there is no outward sign of this change. Moreover, since temperature makes very little difference to the time that elapses before the onset of the climacteric rise, cool weather after the fruit is gathered is of little advantage to the grower who has difficulty in storing his fruit without delay.

In this experiment the composition of the internal atmosphere of the fruit was determined at intervals during the period of delay at 53·5° F. before gas storage, and readings were continued on the same fruits in air at this temperature until they were over-ripe. The results are presented in Table VIII. As was to be expected, the percentage of carbon dioxide in the internal atmosphere of the fruit rose with increasing rate of carbon dioxide-production during the climacteric rise. There was also increasing resistance to the escape of carbon dioxide and to the entry of oxygen as the fruit ripened.

TABLE VIII.

Internal atmosphere of Conference pears in relation to their maturity and respiratory activity at 12° *C.* (*Gathered* 19.9.38.)

Time after gathering (days).	Condition of fruit.	Respiratory activity (cc. CO_2 per 10 kg./hr.).	Internal atmosphere.	
			Carbon dioxide %	Oxygen %
5	Hard, green	43	1·81	18·92
14	Green	105	2·79	17·90
21	Greenish yellow, softening	137	5·36	15·50
25	Ripe, yellow			
28	Over-ripe	151	6·06	13·48
35	Mealy	129	6·43	12·60
42	Soggy, brown	86	9·30	7·50
45	.. ..	71	11·79	4·47
50	Contents liquid	44	31·00	0·00

V. DOYENNÉ DU COMICE PEARS (1934-35).

GATHERING.

Three gatherings were made off uniform trees grown on a good loam soil over brick earth at Faversham, Kent. The date of the last picking approximated to the normal date for gathering this variety. At this date the pears were still very hard and green and contained large quantities of starch. The method adopted in the selection of the fruits was similar to that used with the Conference pears described above.

The average weights and average values for hardness, determined on 100 fruits, were as follows:

Date of gathering.	*Average weight.* (g.)	*Average hardness* (lb. pressure on penetrometer)
18.9.34	118	14·0
25.9.34	137	11·4
2.10.34	159	12·0

Chemical analyses of samples of the fruit immediately after gathering gave the following results, expressed as percentages of original fresh weight:

	Glucose.	*Fructose.*	*Sucrose.*	*Acidity as malic acid.*	*Alcohol-insoluble residue.*
1st gathering	1·172	5·990	0·764	0·362	5·965
2nd gathering	1·301	6·340	0·943	0·237	5·092
3rd gathering	1·078	6·269	1·139	0·223	4·915

The respiratory activity of six fruits, from the time of gathering onwards, was determined individually at 12° C. (53·6° F.). The data are summarized in Table IX. It will be seen that in all three cases the fruit was gathered in the pre-climacteric condition.

TABLE IX.

Respiratory activity at 12° C. (53·6° F.) of Comice pears (1934).

	Respiratory activity ($cc.\ CO_2$/10 kg. hr.).			Days from gathering to pre-climacteric minimum.	Duration of climacteric rise (days).
	Immediately after gathering.	Pre-climacteric minimum.	Climacteric maximum.		
1st pick ..	65	—	—	—	—
2nd pick ..	55	40	135	20	45 (approx.)
3rd pick ..	45	42	130	8	31 (approx.)

SAMPLING, ETC., AND CONDITIONS OF STORAGE.

The sampling methods and the storage conditions were identical with those used for the Conference pears described above.

A. STORAGE IN AIR.

THE RELATION BETWEEN TEMPERATURE AND MEAN DURATION OF LIFE IN AIR.

In relation to temperature, Comice pears were found to behave very similarly to the Conference variety (Table X and Fig. 3). They ripened normally at all the storage temperatures tested except the lowest (34° F.), at which browning of

the flesh (low temperature breakdown) became apparent after about five months' storage. In these experiments good results were obtained with fruit removed from 34° F. to suitable ripening temperatures (64·5°, 53·6°, and 45·5° F.) until the middle of January. Later experiments with this variety, the results of which are dealt with below, show that an extension of the storage life until the early part of February can be obtained in air by the use of a lower storage

TABLE X.

Mean storage life of Doyenné du Comice pears, stored in air immediately after gathering, and ripened at the temperature of storage, 1934-35.

Date of gathering.	Temperature of storage. °F.	Temperature of storage. °C.	Dates when eating-ripe.	Average storage life (days).
1st gathering (18.9.34)	64·4	18·0	28.10.34	40
	53·6	12·0	4.11.34	47
	45·5	7·5	12.11.34	55
	41·0	5·0	27.11 to 6.12.34	75
	37·4	3·0	10. 1.35	114
	33·8	1·0	did not ripen normally at this temperature.	
2nd gathering (25.9.34)	64·4	18·0	27.10.34	32
	53·6	12·0	2.11.34	38
	45·5	7·5	12.11.34	48
	41·0	5·0	27.11 to 6.12.34	68
	37·4	3·0	10. 1.35	107
	33·8	1·0	did not ripen normally at this temperature.	
3rd gathering (2.10.34)	64·4	18·0	24.10.34	22
	53·6	12·0	1.11.34	30
	45·5	7·5	13.11.34	42
	41·0	5·0	26.11 to 5.12.34	60
	37·4	3·0	10. 1.35	100
	33·8	1·0	did not ripen normally at this temperature.	

temperature, viz. 31·5° F. If cold storage is not employed, Comice pears can be stored in air for the market for periods up to about five weeks.

In most cases all the fruits that ripened at any given temperature became eating-ripe almost simultaneously. The pears kept at 41° F. were an exception to this rule. A scatter of nine days was observed in the ripening of the Comice pears kept at this temperature. No reason can yet be given for this.

As in Conference, the actual date of gathering did not markedly affect the date on which the Comice pears became eating-ripe. It was also confirmed that early gathering results in poor quality in the ripened fruit.

VI. DOYENNÉ DU COMICE PEARS (1937-38).

GATHERING.

A single gathering was made on September 27th, 1937, off the same trees as those used for the 1934-35 experiments. This date was approximately the normal one for the variety. When gathered, the pears were hard (13 lb. pressure on penetrometer), green (colour value 4·5 on the Ditton Laboratory's scale) and showed traces of starch just beneath the skin.

Measurements of respiratory activity were carried out at 53·6° F. (12° C.) on six fruits individually from the time of gathering. The interval between

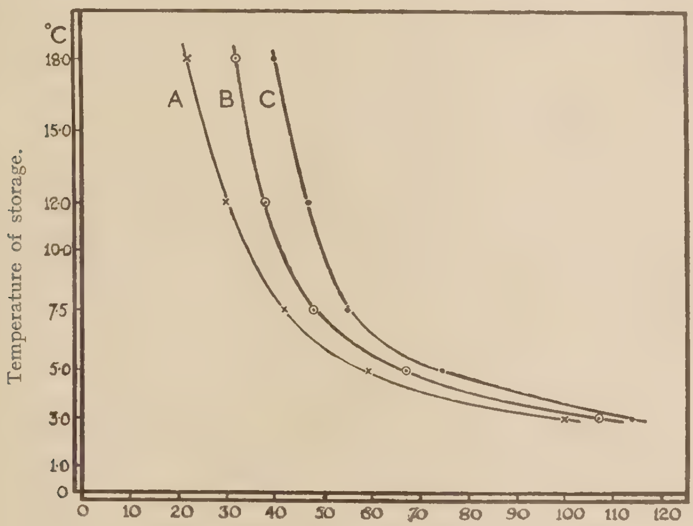

FIG. 3.

Days to ripen in storage.

Temperature and storage life of Doyenné du Comice pears.

A. First gathering (18.9.34).
B. Second gathering (25.9.34).
C. Third gathering (2.10.34).

picking and the beginning of the climacteric rise was unexpectedly short, viz. only three days ; the duration of the climacteric rise was about twenty days and the values for the pre-climacteric minimum and for the climacteric maximum were 48 and 124 cc. of carbon dioxide per 10 kilograms per hour respectively. The pears were judged to be suitable for gas storage since they were gathered in the pre-climacteric condition and were stored within a few hours of gathering.

SAMPLING.

The sampling method was the same as that used for the Comice pears of the 1934-35 season. Each sample consisted of twenty unwrapped fruits.

A. Refrigerated gas storage.

Conditions of storage.

The samples of fruit were stored under the following conditions:

Atmosphere.	*Oxygen* (%).	*Carbon dioxide* (%).	*Nitrogen* (%).
1	2·5	5·0	92·5
2	2·5	10·0	87·5
3	5·0	5·0	90·0
4	5·0	10·0	85·0
5	10·0	10·0	80·0
6	16·0	5·0	79·0
7 (synthetic air)	21·0	0·0	79·0

Atmospheres 4 and 6 were used at 34° F. (1·1° C.) only, the others at both 34° F. (1·1° C.) and 31·5° F. (—0·25° C.).

With the exception of atmosphere 6, which was obtained by the method of restricted and controlled ventilation, all the gas mixtures were made up by mixing the pure gases in the desired proportions and metering them through the storage cabinets at the required rate. In all cases the atmospheres were conditioned to approximately 90 per cent. relative humidity before entering the cabinets.

Ripening temperatures.

Comice pears will not ripen normally at temperatures as low as 34° F. (1·1° C.) whatever atmospheric conditions are employed. In order to compare the effects of the various storage conditions tested, therefore, samples of fruit were removed to air to ripen at 50° F. (10° C.) and at 65° F. (18·3° C.). The fruit ripened normally at both temperatures and its quality, when ripe, was satisfactory in both cases.

Gas storage results: comparison of atmospheric conditions.

The storage results are set out in Table XI. Of the two temperatures tested, viz. 34° F. and 31·5° F., only the lower one can safely be recommended for gas storage, owing to the liability of the fruit to develop brown heart at the higher temperature. Of the atmospheres tested, atmosphere 2 (10 per cent. carbon dioxide, 2·5 per cent. oxygen, and 87·5 per cent. nitrogen) gave the best result. The maximum storage life obtained in this atmosphere was approximately five months, as compared with four months in air (atmosphere 7) at the same temperature. It should be noted, however, that the gas stored fruit at 31·5° F., when removed to air at the end of its storage life (i.e. after 150 days), took twelve days to ripen at 65° F., whereas the air stored fruit at the same

TABLE XI.

Time (in days) taken to ripen at 65° F. (18·3° C.) by gas stored and cold stored Doyenné du Comice pears, and their quality when eating-ripe. (Fruit gathered 27.9.37.)

Storage temperature.	Days in store.	Composition of atmosphere.						
		Atmosphere 1.	Atmosphere 2.	Atmosphere 3.	Atmosphere 4.	Atmosphere 5.	Atmosphere 6.	Atmosphere 7.
		CO_2 5·0% O_2 2·5% N_2 92·5%	CO_2 10·0% O_2 2·5% N_2 87·5%	CO_2 5·0% O_2 5·0% N_2 90·0%	CO_2 10·0% O_2 5·0% N_2 85·0%	CO_2 10·0% O_2 10·0% N_2 80·0%	CO_2 5·0% O_2 16·0% N_2 79·0%	CO_2 0·0% O_2 21·0% N_2 79·0%
31·5° F. (−0·25° C.)	57	11·5 g.	12·0 g.	11·0 g.		12·0 f.		8·0 g.
	97	11·5 g.	12·5 g.	(11·0) g.		12·0 f.		7·0 g.
	121							6·0 f.
	150	11·5 f.	12·0 g.	(11·5) f.		(11·5) f.		did not ripen normally.
	188	(10·0) f.	(12·0) f.	(10·0) f.		(11·0) f.		
	213	(10·0) f.	(12·0) f.	(10·0) f.		(10·0) f.		
34° F. (1·1° C.)	57	9·5 g.	12·0 f.	9·0 g.	9·0 g.	10·0 f.	9·0 g.	7·5 g.
	97	(9·0) g.	12·0 f.	8·0 g.	8·0 g.	(10·0) f.	7·0 g.	5·5 g.
	121							did not ripen normally.
	150	(8·0) g.	(11·0) f.	(8·0) g.	(9·0) f.	(10·0) f.	(6·5) f.	
	188	(6·0) f.		(6·0) f.	did not ripen normally.	(10·0) f.	did not ripen normally.	
	213	did not ripen normally.		did not ripen normally.				

g. = good. f. = fair.
Note.—Brackets indicate that wastage exceeded 10 per cent. when the fruit was eating-ripe.

temperature, removed from storage at the end of its storage life (i.e. after 121 days), ripened at 65° F. in six days. Even after much shorter periods of storage, gas stored fruit took considerably longer to ripen after removal than fruit cold stored in air. For example, after two months' storage, gas stored fruit ripened in twelve days, as compared with eight days for cold stored fruit, the ripening temperature being 65° F. in each case. Gas stored pears can, therefore, be relied upon to stand up well during distribution, even after long periods of storage.

The main cause of the comparatively short life of these Comice pears under the gas storage conditions tested, was the development of brown heart (Plate III, Fig. 6). In atmosphere 2 at 31·5° F., however, only 5 per cent. of the pears showed signs of this disease when examined at the beginning of April, that is, after more than six months' storage. At the higher temperature (34·0° F.) this trouble was far more serious (Table XII). In view of these results a further series of tests were carried out in 1939-40 at 31·5° F. (see below) to ascertain the effect of concentrations of carbon dioxide lower than 5 per cent., combined with low percentages of oxygen; but no extension of storage life beyond five months was obtained by the use of any of the gas mixtures tested in these later experiments.

Under most of the storage conditions tested a few fruits showed dark brown areas on the skin with discoloration of the underlying flesh. These were typical examples of pear scald (see Plate IV, Figs. 7 and 8).

Changes in colour and hardness during storage.

The pears stored in air at 31·5° F. (—0·25° C.) showed during their storage life (121 days) a decrease in the value for hardness from 13 lb., the value when gathered, to 9 lb. During this period the initial green ground-colour of the fruit (value 4·5 on Ditton Laboratory's Colour Scale) had become lighter (value 5·5), but no definite yellowing had occurred. When the fruit had reached the eating-ripe stage after removal to higher temperatures the value for hardness was 2 lb. and that for the ground-colour 8·5 to 9. The gas stored fruit at 31·5° F. temperature did not soften appreciably throughout its storage life (150 days) and showed even less change in ground-colour than the controls in air.

An interesting point concerning the ripening of the gas stored fruit after removal from storage was that while there was a marked uniformity in the degree of softening and development of juiciness, there was a considerable amount of individual variation in the degree of yellowing, some fruits ripening yellowish-green and others yellow. The air stored fruit and the gas stored fruit that ripened yellow had a more pronounced pear aroma and flavour than the gas stored pears that were yellowish-green when ripe.

TABLE XII.

Brown heart in gas stored Comice pears (1937-38).

Storage temperature.	Days in storage.	Percentage of fruits showing brown heart.						
		Atmosphere 1.	Atmosphere 2.	Atmosphere 3.	Atmosphere 4.	Atmosphere 5.	Atmosphere 6.	Atmosphere 7.
		CO_2 5·0 O_2 2·5 N_2 92·5	CO_2 10·0 O_2 2·5 N_2 87·5	CO_2 5·0 O_2 5·0 N_2 90·0	CO_2 10·0 O_2 5·0 N_2 85·0	CO_2 10·0 O_2 10·0 N_2 80·0	CO_2 5·0 O_2 16·0 N_2 79·0	CO_2 0·0 O_2 21·0 } Air N_2 79·0
31·5° F. (−0·25° C.)	97 ..	0·0	0·0	0·0		0·0		0·0
	150 ..	0·0	0·0	2·5		10·0		0·0
	180 ..	35·0	5·0	32·0		50·0		0·0
34° F. (1·1° C.)	97 ..	0·0	2·5	0·0	5·0	25·0	0·0	0·0
	150 ..	0·0	33·0	22·0	65·0	40·0	10·0	0·0
	180 ..	66·0	75·0	58·0	83·0	74·0	68·0	0·0

TABLE XIII.

Time (in days) taken to ripen at 65° F. (18·3° C.) by gas stored and cold stored Doyenné du Comice pears, and their quality when eating-ripe. (*Fruit gathered* 2.10.39.)

Storage temperature.	Days in store.	Composition of atmosphere.							
		Atmosphere 1.		Atmosphere 2.		Atmosphere 3.		Atmosphere 4.	
		CO_2 0·0% O_2 21·0% N_2 79·0%		CO_2 3·0% O_2 2·5% N_2 94·5%		CO_2 5·0% O_2 2·5% N_2 92·5%		CO_2 3·0% O_2 5·0% N_2 92·0%	
31·5 F. (−0·25° C.)	80	7	g.	11	g.	11	g.	11	g.
	104	7	g.	11	g.	11	g.	11	g.
	132	(8)	p.	12	g.	12	f.	11	f.
	153	did not ripen normally.		11	f.	(12)	f.	11	f.
	188	—		(11)	f.	(11)	p.	(11)	p.

g. = good. f. = fair. p. = poor.
Note 1.—Brackets indicate that wastage exceeded 10 per cent. when the fruit was eating-ripe.
Note 2.—Fruit assessed as poor should not be marketed, although there may be nothing in its appearance on removal from store to warn the grower of its poor quality.

VII. DOYENNÉ DU COMICE PEARS (1939-40).

Under the various conditions tested in 1937-38 the development of brown heart was found to be the limiting factor in the refrigerated gas storage of Comice pears. Since all the atmospheres used in these tests contained at least 5 per cent. of carbon dioxide it was decided to conduct further experiments with this variety, using gas mixtures containing low concentrations of both oxygen and carbon dioxide.

Gathering.

A single gathering was made on October 2nd, 1939, off the same trees as those used in the 1934 and 1937 experiments. The pears, which contained much starch, were green (value 5 on the Ditton Laboratory's Scale) and firm (11·5 lb. pressure on the penetrometer), and were in the pre-climacteric condition, as was shown by the results of determinations of the CO_2-production of six pears determined individually in air at 53·6° F. (12° C.) from the time of gathering onwards.

Sampling.

The usual method was employed, each sample consisting of twenty fruits.

A. Refrigerated gas storage.

Conditions of storage.

The samples of fruit were stored at 31·5° F. (—0·25° C.) in the following gas mixtures:

Atmosphere.	*Oxygen* (%).	*Carbon dioxide* (%).	*Nitrogen* (%).
1 (air)	21·0	0·0	79·0
2	2·5	3·0	94·5
3	2·5	5·0	92·5
4	5·0	3·0	92·0

Gas storage results: comparison of atmospheres.

The storage results are shown in Table XIII. The longest storage life, about five months, was obtained in atmospheres 2 and 4, both of which contained 3 per cent. of carbon dioxide with 2·5 per cent. and 5 per cent. of oxygen respectively. This storage life was the same as the longest obtained in 1937-38 in an atmosphere consisting of 10 per cent. of carbon dioxide, 2·5 per cent. of oxygen and 87·5 per cent. of nitrogen. In air the fruit kept satisfactorily for about 3½ months, as compared with 4 months for fruit kept under similar conditions in 1937-38. It would appear, therefore, that the lower percentages of carbon dioxide combined with the low percentages of oxygen used in the present

experiments produce results which, from the practical point of view, are little better than those obtained previously in an atmosphere containing 10 per cent. of carbon dioxide and 2·5 per cent. of oxygen.

It is interesting to note that in spite of the low concentrations of carbon dioxide used, a certain amount of brown heart developed in gas storage late in the storage life of the fruit. In addition, a diffused browning of the flesh immediately beneath the skin, but not externally visible, occurred to a limited extent, especially in atmosphere 3 (5 per cent. carbon dioxide, 2·5 per cent. oxygen, and 92·5 per cent. nitrogen). This type of functional disease was not observed in the previous experiments. Towards the end of these tests a few fruits showed typical scalding of the skin.

As before, little change in hardness of the flesh or in ground-colour occurred in gas storage.

VIII. WILLIAMS' BON CHRÉTIEN PEARS (1935-36 and 1936-37).

Storage trials with Williams' bon Chrétien pears were carried out in the seasons 1935-36 and 1936-37. The fruit was gathered off the same trees and on the same date (August 26th) in both seasons, the usual precautions being taken as regards handling, sampling, etc.

Data for the condition of the pears when gathered are given in Table XIV. It will be seen that in both seasons the fruit was gathered in the pre-climacteric condition and was, therefore, suitable for gas storage.

TABLE XIV.

Data for Williams' bon Chrétien pears at the time of gathering.

Date of gathering	Average weight per fruit (g.).	Average hardness (lb. pressure on penetrometer).	Respiratory activity at 53·6° F. (12° C.).				
			CO_2-production (cc. CO_2/10 kg./hr.).			Days from gathering to pre-climacteric minimum	Duration of climacteric rise (days).
			Immediately after gathering.	Pre-climacteric minimum.	Climacteric maximum.		
26.8.1935	135	22·5	90	78	255	6	16
26.8.1936	133	23·5	65	60	188	5	12

A. STORAGE IN AIR.

CONDITIONS OF STORAGE (1935-36).

Samples of fruit (20 pears per sample) were stored in air within a few hours of gathering at seven constant temperatures between 75° F. (24° C.) and 34° F. (1·1° C.). At each temperature samples of fruit were stored in trays stacked

in the open in constant temperature rooms. The stacks of trays were covered with damp towelling. At intervals of approximately one month samples were transferred from the two lowest temperatures (41° and 34° F.) to air at 64·5° F. (18° C.), 59° F. (15·0° C.), and 53·5° F. (12° C.) in order to ripen.

CONDITIONS OF STORAGE (1936-37).

Seven constant temperatures between 70° F. (21° C.) and 31·5° F. (−0·25° C.) were used. The other conditions of storage were similar to those of the previous season except that at the three lowest temperatures the fruit was kept in metal cabinets ventilated with fresh air from outside the building. The air was conditioned to about 90 per cent. relative humidity before it entered the cabinets.

The temperatures used for ripening were 70° F. (21° C.), 60° F. (15·5° C.), and 50° F. (10° C.).

THE RELATION BETWEEN TEMPERATURE AND MEAN DURATION OF LIFE IN AIR.

In contrast with the Conference and Doyenné du Comice pears which ripened normally at all temperatures tested between 64·5° F. (18° C.) and 37·5° F. (3° C.), but not at 34° F. (1·1° C.), the Williams' pears ripened normally at the temperatures tested between 75° F. (24° C.) and 48·5° F. (9·5° C.), but not at 41° F. (5° C.) or at lower temperatures. The lower limit of temperature for normal ripening of these pears was thus somewhere between 41° F. and 48·5° F. as compared with a temperature between 34° F. and 37·5° F. for the Comice and Conference varieties. In no case was there any rotting of the fruit by fungi before the eating-ripe stage was reached. Taking, as before, the mean storage life as the point at which 50 per cent. of the fruit is eating-ripe according to three independent judgments, the results with Williams' pears for the two seasons are as shown in Table XV.

The behaviour of the pears when stored at temperatures below those at which they will ripen normally is very similar to that of the Conference pears described above. They soften slowly and eventually begin to yellow, but the softening that occurs is far less than that of fruit in the eating-ripe condition. They sweeten, but the sweetening is accompanied by an abnormal flavour. Next, the flesh of the fruit turns brown, and finally browning of the skin also occurs. The lower the temperature, the less the fruit softens before browning occurs. Pears kept at low temperatures for a certain time will ripen quite normally when removed to higher temperatures. Then follows a period during which the fruit, although still appearing sound at the low temperature, will not ripen normally on removal to any higher temperature.

The effect of the ripening or conditioning temperature on quality (texture, flavour, etc.) is more pronounced in Williams' pears than in Conference or

TABLE XV.

Mean storage life of Williams' bon Chrétien pears stored in air immediately after gathering, and ripened at the temperature of storage.

Date of gathering.	Temperature of storage.		Date when ripe.	Average life at storage temperature (days).
	°F.	°C.		
26.8.1935	75·0	24·0	7.9.35	12·5
	64·5	18·0	11.9.35	16·0
	59·0	15·0	14.9.35	19·0
	53·5	12·0	17.9.35	21·5
	48·5	9·5	20.9.35	24·5
	41·0	5·0	did not ripen normally at this temperature	—
	34·0	1·0	do.	—
26.8.1936	70·0	21·0	6.9.35	11·0
	60·0	15·5	11.9.35	16·0
	50·0	10·0	17.9.35	21·5
	40·0	4·5	did not ripen normally at this temperature.	—
	37·0	3·0	do.	—
	34·0	1·0	do.	—
	31·5	−0·25	do.	—

Doyenné du Comice. The best results were obtained between 59° and 65° F. 50° F. was certainly too low for the development of high quality.

The periods for which the pears could be kept at the low temperatures and still ripen normally on removal to a temperature of 60° F. and the times that elapsed before the commencement of browning of the flesh, are shown in Table XVI.

It appears, therefore, that a storage life of more than seven to eight weeks cannot be relied upon for home-grown Williams' pears in cold storage in air

TABLE XVI.

Ripening of Williams' bon Chrétien pears after storage.

Date of gathering.	Storage temperature.	Ripened normally on removal to higher temperature after	Failed to ripen normally on removal to higher temperature after	Internal browning in store began after
26.8.35	41°F (5° C.)	—	35 days	44 days
	34° F. (1·1° C.)	51 days	70 days	170 days
26.8.35	37·5° F. (3·0° C.)	37 days	48 days	60 days
	34° F. (1·1° C.)	48 days	70 days	125 days
	31·5° F. (−0·25° C.)	106 days	148 days	221 days

at 34° F. It should be stressed again that when attempting to push cold storage to its limit, there is no obvious means of determining from the appearance of the fruit whether or not it has actually reached the stage at which it will either fail to ripen or will ripen abnormally with internal and external browning when placed on the market. In such circumstances the grower would be well advised to remove samples of fruit from store at intervals for a ripening test at 60° to 65° F.

A temperature as low as 31·5° F. can safely be used with considerable advantage in lengthening storage.

B. Refrigerated gas storage.

Conditions of storage (1935-36).

The gas stored samples (each containing twenty fruits) were kept at one temperature only, 34° F. (1·1° C.), in atmospheres of the following composition maintained by the continuous flow method :

Atmosphere.	*Oxygen %.*	*Carbon dioxide %.*	*Nitrogen %.*
1	10·0	10·0	80·0
2	2·5	10·0	87·5
3	5·0	5·0	90·0
4	2·5	5·0	92·5
8	21·0	0·0	79·0 (synthetic air)

Fruit was also stored in a gas mixture similar in composition to atmosphere 1, but obtained by the method of restricted and controlled ventilation.

The pears were stored on trays in metal cabinets through which the artificial gas mixtures were passed at a known rate. All these atmospheres, before entering the cabinets, were conditioned to approximately 90 per cent. relative humidity. The fruit was unwrapped.

At least three samples were removed from each set of storage conditions on the following dates : October 16th, November 11th and December 9th, 1935, and January 6th, February 12th and March 18th, 1936.

The ripening temperatures used were 53·5° F. (12° C.), 59° F. (15° C.), and 64·5° F. (18° C.).

Gas storage results (1935-36) : comparison of atmospheres.

The time taken to ripen in air at 59° F. by Williams' pears after removal from gas storage and their quality when ripe are given in Table XVII. It may be concluded from this season's results that Williams' pears can be gas stored satisfactorily at 34° F. under all the gas storage conditions tested. The pears stored in atmospheres 2 and 3 kept in good condition for a period of five months

TABLE XVII.

Time (in days) taken to ripen at 59° F. (15° C.) by gas stored and cold stored Williams' bon Chrétien pears, and their quality when eating-ripe. (Fruit gathered 26.8.35.)

Storage temperature.	Days in store.	Composition of atmosphere. Atmosphere 1.		Atmosphere 2.		Atmosphere 3.		Atmosphere 4.		Atmosphere 8.
		CO_2 10·0%, O_2 10·0%, N_2 80·0%		CO_2 10·0%, O_2 2·5%, N_2 87·5%		CO_2 5·0%, O_2 5·0%, N_2 90·0%		CO_2 5·0%, O_2 2·5%, N_2 92·5%		CO_2 0·0%, O_2 21·0%, N_2 79·0% } Air
34° F. (1·1° C.)	51	—		—		—		—		8 g. did not ripen normally.
	85	10	g.	12	g.	7	v.g.	10	g.	
	105	10	g.	12	g.	7	v.g.	9	g.	
	133	10	g.	(11)	g.	(6)	g.	9	g.	
	170	10	g.	(10)	g.	(6)	g.	8	g.	
	205	9	g.					8	g.	

v.g. = very good. g. = good.

Note.—Brackets indicate that wastage exceeded 10 per cent. when the fruit was eating-ripe.

TABLE XVIII.

Changes in hardness of flesh of Williams' bon Chrétien pears (lb. pressure on penetrometer) during storage in various atmospheres at 34° F. The hardness on gathering (26.8.35) was 22·5 lb.

Days in storage.	Composition of atmosphere. Atmosphere 1.	Atmosphere 2.	Atmosphere 3.	Atmosphere 4.	Atmosphere 8.
	CO_2 10·0%, O_2 10·0%, N_2 80·0%	CO_2 10·0%, O_2 2·5%, N_2 87·5%	CO_2 5·0%, O_2 5·0%, N_2 90·0%	CO_2 5·0%, O_2 2·5%, N_2 92·5%	CO_2 0·0%, O_2 21·0%, N_2 79·0% } Air
51	22·2	21·0	20·8	20·6	21·9
85	21·0	20·7	22·0	19·4	16·4
105	19·9	19·5	22·6	20·0	12·5
133	22·3	20·6	22·0	22·0	12·7
170	20·0 (21·3)*	18·7	16·9	18·8	—
205	19·5	18·9	9·1	20·6	—

* The value in brackets is for fruit stored by the method of restricted ventilation.

or more. In the other two atmospheres the fruit was of good quality when removed from gas storage after about seven months. As noted above, the fruit stored in air was useless for the market after, at the most, two months' storage at 34° F.

Williams' pears ripened very satisfactorily at 59° F. and at 64·5° F. Not only was the quality of the ripe fruit better at these temperatures than at 53·5° F., but the wastage was less. This point was brought out even more clearly in the course of the 1936-37 experiments.

No brown heart in the gas stored fruit was observed at any examination.

Changes in hardness of flesh.

Determinations of the hardness of the fruit were made on samples removed from store at intervals throughout these tests. Table XVIII gives the values for hardness at gathering and on the various dates of removal from store. At 34° F. the pears stored in air began to soften noticeably after 50 days, those in atmosphere 3 after about 130 days, while those stored in atmospheres containing lower concentrations of oxygen or higher concentrations of carbon dioxide, viz. atmospheres 1, 2 and 4, had not softened appreciably by the end of the experiment, that is, after approximately seven months' storage.

Records were also obtained of the rate of softening of fruit when removed from gas storage (10 per cent. carbon dioxide, 10 per cent. oxygen, and 80 per cent. nitrogen) after 170 days. Fig. 4 shows the rate of softening of these pears in air at 67·5° F., at 59° F., and at 53·5° F. They reached the eating-ripe condition (hardness value about 2·5 lb. pressure) after 6, 9 and 12 days respectively.

Conditions of storage (1936-37).

The method employed was similar to that of the previous season, but a wider range of storage temperatures was tested, viz. 31·5° F. (—0·25° C.), 34° F. (1·1° C.), and 37° F. (2·8° C.). The atmospheres tested were those used in 1935-36 with the addition (at 34° F. only) of the following :

Atmosphere.	*Oxygen %.*	*Carbon dioxide %.*	*Nitrogen %.*
5	10·0	5·0	85·0
6	2·5	3·0	94·5
7	2·5	0·0	97·5

As an additional control at 34° F. fruit was kept in a cabinet through which air from outside the building was passed. Synthetic air, made up in the same way as the gas mixtures, was tested at all three temperatures. No significant differences were observed between the fruit stored in normal air and that stored in synthetic air.

Samples were removed from each set of conditions to ripening rooms on the following dates: October 13th, November 19th, and December 10th, 1936; January 21st, February 15th, and March 12th, 1937. The temperatures used for ripening were 50° F. (10° C.), 60° F. (15·5° C.), and 70° F. (21·1° C.).

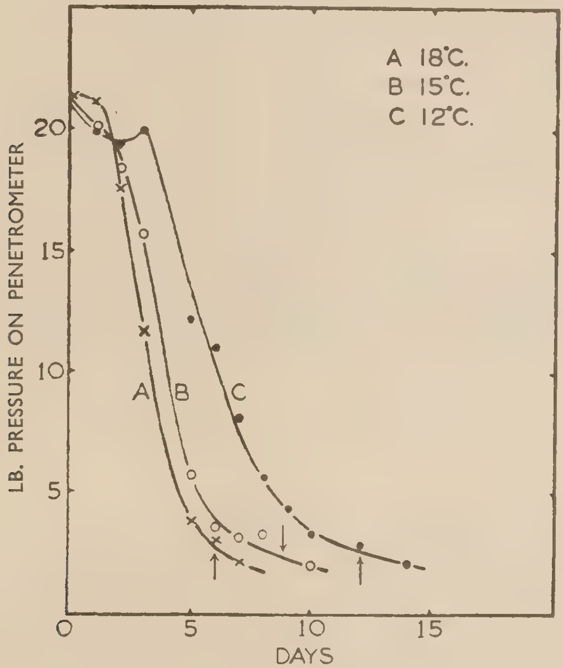

FIG. 4.

Softening of Williams' bon Chrétien pears removed to higher temperatures for ripening after 170 days' gas storage in 10 per cent. carbon dioxide + 10 per cent. oxygen + 80 per cent. nitrogen at 34° F.

Note.—Arrows indicate the time at which the fruits were eating-ripe.

GAS STORAGE RESULTS (1936-37): COMPARISON OF ATMOSPHERES.

The results obtained in the various atmospheres at the three storage temperatures are presented in Table XIX. This shows the time taken to ripen in air at 60° F. after removal from storage, and the quality of the pears when eating-ripe. The best results were obtained at the lowest storage temperature (31·5° F.). At this temperature, atmosphere 1 (10 per cent. carbon dioxide, 10 per cent. oxygen, and 80 per cent. nitrogen) proved the most satisfactory. Atmosphere 3, although better than air, was not so good as atmospheres 2 and 4. At 34° and 37° F. the best results were obtained in atmosphere 2.

TABLE XIX.

Time (in days) taken to ripen at 60° F. (15·5° C.) by gas stored and cold stored Williams' bon Chrétien pears, and their quality when eating-ripe. (*Fruit gathered* 26.8.36.)

Storage temperature.	Days in store.	Composition of atmosphere. Atmosphere 1. (CO_2 10·0%, O_2 10·0%, N_2 80·0%)	Atmosphere 2. (CO_2 10·0%, O_2 2·5%, N_2 87·5%)	Atmosphere 3. (CO_2 5·0%, O_2 5·0%, N_2 90·0%)	Atmosphere 4. (CO_2 5·0%, O_2 2·5%, N_2 92·5%)	Atmosphere 5. (CO_2 5·0%, O_2 10·0%, N_2 85·0%)	Atmosphere 6. (CO_2 3·0%, O_2 2·5%, N_2 94·5%)	Atmosphere 7. (CO_2 0·0%, O_2 2·5%, N_2 97·5%)	Atmosphere 8. (CO_2 0·0%, O_2 21·0%, N_2 79·0%) Air
31·5° F. (−0·25° C.)	48	12·0 g.	13·0 g.	12·0 f.	12·0 g.				8·0 g.
	85	11·0 g.	11·0 g.	9·0 f.	11·0 g.				8·0 f.
	106	11·0 g.	11·0 g.	9·5 f.	11·0 g.				(10·0) f.
	148	13·0 g.	(13·0) g.	(11·5) f.	12·0 g.				failed to ripen normally.
	173	15·0 g.	(13·0) g.	(12·0) f.	(13·0) f.				
	198	13·0 f.	(12·0) f.	(11·0) f.	(11·0) f.				
34° F. (1·1° C.)	48	10·5 g.	11·0 g.	11·0 g.	11·0 g.	10·5 g.	10·0 f.	(8·0) p.	(7·0) f.
	85	11·5 g.	12·0 g.	8·0 g.	9·0 g.	(10·0) f.	(10·0) f.	—	(8·0) p.
	106	11·0 g.	11·0 g.	9·5 f.	10·0 g.	(9·5) f.	(8·0) f.	—	failed to ripen normally.
	148	(11·0) g.	12·0 g.	(10·0) f.	(10·0) g.	(10·0) f.	—	—	
	173	(11·0) f.	(11·5) f.	(10·0) f.	(11·0) f.	(11·0) p.	—	—	
	198	(9·5) f.	(11·0) f.	failed to ripen normally.	(8·0) f.	failed to ripen normally.	—	—	
37° F. (2·8° C.)	48	10·0 g.	10·0 g.	9·0 f.	10·0 f.				failed to ripen normally.
	85	9·0 g.	10·0 g.	(8·0) f.	(9·0) f.				
	106	8·0 g.	10·0 g.	(7·0) f.	(8·0) f.				
	148	9·0 f.	10·0 g.	failed to ripen normally.	(9·0) f.				
	173	(10·0) f.	(11·0) f.		failed to ripen normally.				
	198	failed to ripen normally.	failed to ripen normally.						

g. = good. f. = fair. p. = poor.

Note 1.—Brackets indicate that wastage exceeded 10 per cent. when the fruit was eating-ripe.

Note 2.—Fruit assessed as poor should not be marketed, although there may be nothing in its appearance on removal from store to warn the grower of its poor quality.

FIG. 1.

Condition of Conference pears after two months' gas storage. Fruit stored immediately after gathering.

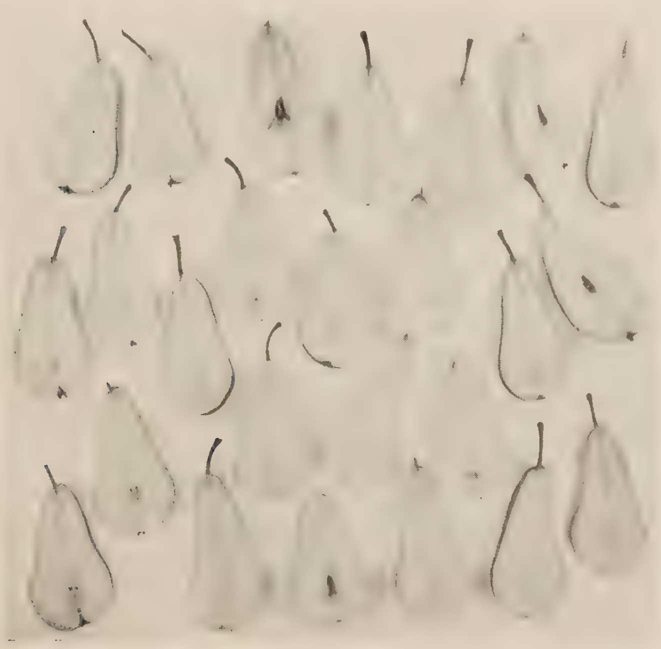

FIG. 2.

Condition of Conference pears after two months' gas storage. Fruit kept for four days in air at 53·5° F. before gas storage.

FIG. 3.

Condition of Conference pears after two months' gas storage. Fruit kept for ten days in air at 53·5° F. before gas storage.

FIG. 4.

Condition of Conference pears after two months' gas storage. Fruit kept for two weeks in air at 53·5° F. before gas storage.

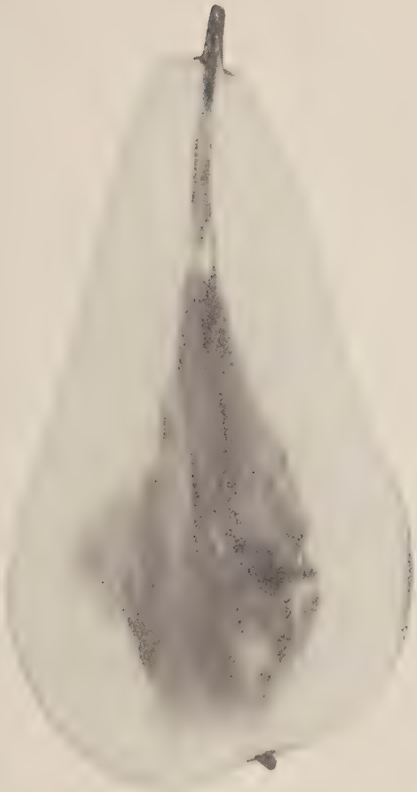

FIG. 5.
Longitudinal section of Conference pear showing core breakdown.

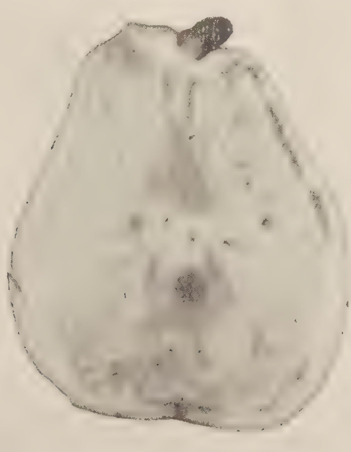

FIG. 6.
Longitudinal section of Comice pear showing severe brown heart.

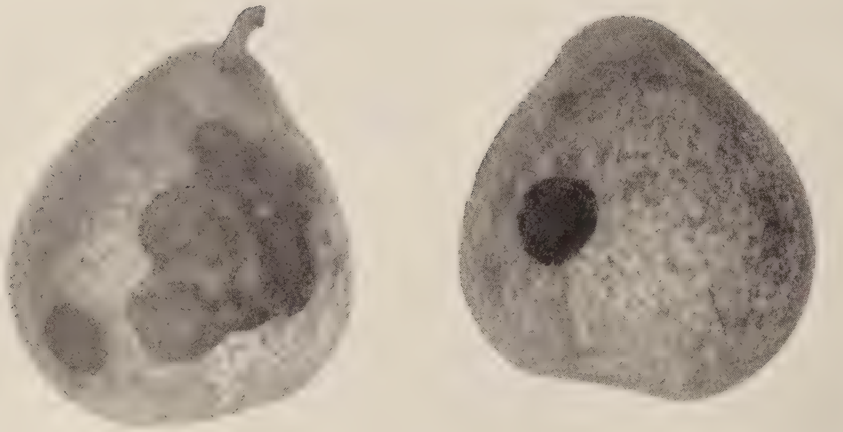

FIG. 7.
Comice pears showing scald.

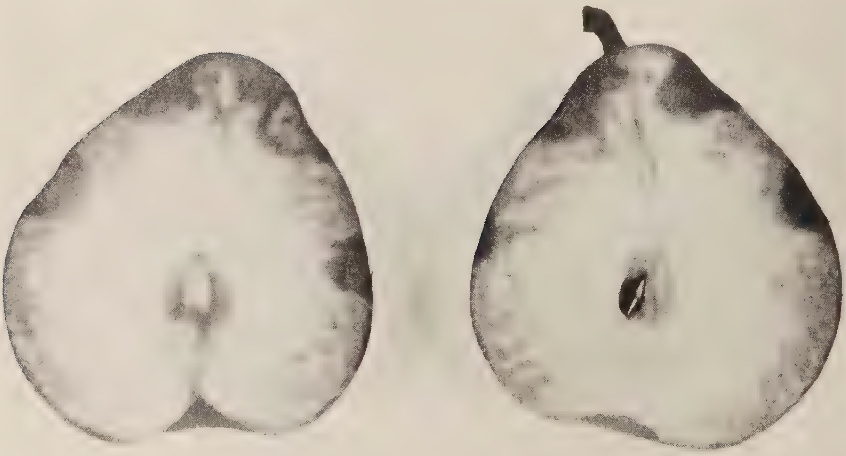

FIG. 8.
Longitudinal sections of Comice pears showing browning of the flesh underlying the scalded areas of the skin.

The condition of the fruit stored in atmospheres 6 and 7, containing only 3 per cent. and traces of carbon dioxide respectively, compared unfavourably with that of fruit stored in all the other gas mixtures tested.

A close inspection of the data shown in Table XIX brings out the relative effect of the various storage variables on the storage life of the fruit. Thus, in the series at 34° F. with percentages of carbon dioxide from 0·5-3-5-10, and with 2·5 per cent. oxygen in each case, it is seen that the concentration of carbon dioxide has an important effect. A difference in the percentage of oxygen over the range 2·5-5-10 per cent. (5 per cent. CO_2 present in each case) has less effect.

The importance of the effect of the ripening temperature on quality has already been stressed. Its effect on wastage is equally important (Table XX). Ripening temperatures below 60° F. should obviously be avoided if possible.

Table XX.

Effect of ripening temperature on extent of wastage due to breakdown in Williams' bon Chrétien pears.

Days in gas storage at 31·5° F.	Percentage wastage during ripening (all gas conditions taken together).		
	Ripened in air at 70° F.	Ripened in air at 60° F.	Ripened in air at 50° F.
85	0·0	1·0	15·0
106	0·0	0·0	14·0
148	4·0	12·5	12·5
173	2·5	17·5	54·0

A small amount of brown heart developed late in the atmospheres containing 10 per cent. carbon dioxide, but only at the two higher temperatures of storage (34° and 37° F.).

The keeping quality of the pears was not quite so good as in the previous season, a maximum storage life in gas storage of five to six months being obtained, as compared with six to seven months in 1935-36. The maximum storage life in cold storage in air was rather less than two months.

Finally, attention may be drawn to a point of practical importance. When the Williams' bon Chrétien pear has begun to ripen and is showing signs of yellowing, the skin is extremely delicate, and even quite gentle handling may result in bruising that is followed by browning of the skin. In the hard, green state in which they are removed from gas storage, the pears can be handled with little risk of bruising the skin.

A study of the respiratory activity of pears has been carried out in connexion with these cold storage and refrigerated gas storage experiments. The results of this study will be presented in the next paper in this series.

The authors wish to acknowledge the valuable assistance of Mr. G. H. Crouch throughout these investigations.

The work described above was carried out as part of the research programme of the Food Investigation Board and is published by permission of the Department of Scientific and Industrial Research.

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APPENDIX.

Since this paper was written a fact of importance in relation to gas storage of pears has come to light. In the season 1941-42 many Conference pears developed without seeds and with only a rudimentary core. This fruit, when fully developed, was found to have a respiratory activity, both in the pre-climacteric and in the climacteric phases, much higher than that normally shown by this variety. It was also found that in gas storage a considerable percentage (33 per cent.) of these seedless pears developed brown heart, even when the concentration of carbon dioxide used was that previously found to give the best results with this variety. These observations clearly need to be followed up.

(*Received* 22/10/41.)

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GROUND COLOUR CHART
FOR
CONFERENCE PEARS

PLATE I

PICKING FOR STORAGE

Pick and store immediately when ground-colour matches Plate I.

(Ditton Colour Standard 4½)

PLATE 2

Pears picked for storage must not be more yellow than Plate 2.

(Ditton Colour Standard 5)

PLATE 3

REMOVAL FROM STORAGE

Remove from cold or gas storage to ripen in air at higher temperatures (50°—60° F.) at the latest when ground-colour matches Plate 3.

(Ditton Colour Standard 5½)

PLATE 4

When ground-colour matches Plate 4 (Ditton Colour Standard 6) **damage to the fruit may have occurred.**

NOTE I. When ground-colour is obscured by russeting, gently scrape away this superficial layer to expose smooth skin beneath.

NOTE II. To avoid fading, keep chart from light when not in use.

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